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ICHTHYOSAURS OF THE BRITISH MIDDLE AND UPPER JURASSIC.

Benjamin C. Moon and Angela M. Kirton

ABSTRACT

The ichthyosaur material of the British Middle and Upper Jurassic is revisited and re-described. Three valid species are present: *Ophthalmosaurus icenicus*, *Brachypterygius extremus*, and *Nannopterygius enthekiodon*. *Macropterygius* sp. indet., with affinities to Platypterygiinae, formerly referred to *Ichthyosaurus trigonus*, is noted based on humeral material. *Grendelius mordax* is synonymized with *Brachypterygius extremus*. *Ophthalmosaurus monocharactus* is synonymized with *Ophthalmosaurus icenicus*. *Ichthyosaurus advena*, *Ichthyosaurus chalarodeirus*, and *Ichthyosaurus hygrodeirus* are rejected as *nomina nuda*, while *Ichthyosaurus aequalis*, *Ichthyosaurus dilatatus*, *Ichthyosaurus ovalis*, *Ichthyosaurus thyreospondylus*, and *Ichthyosaurus trigonus* are rejected as *nomina dubia*. The majority of remains are from the Oxford Clay and Kimmeridge Clay formations, but ichthyosaur material is found throughout the Aalenian–Portlandian interval.

The affinities of *Baptanodon* are considered, and it appears to represent a species of *Ophthalmosaurus*: *Ophthalmosaurus natans*. Diagnostic characters are considered important to separate this from *Ophthalmosaurus icenicus* at only the species level. The palaeobiogeographical distribution of Ophthalmosauridae suggests an early Middle Jurassic

origin in the south-eastern Pacific Ocean, with a rapid spread to the Tethys Ocean by the Bathonian.

Les ichtyosaures du jurassique moyen et supérieur britannique.

RÉSUMÉ

Le matériel d'ichtyosaure du Jurassique moyen et supérieur de la Grande-Bretagne est examiné et décrit de nouveau. Trois espèces valides sont présentes: *Ophthalmosaurus icenicus*, *Brachypterygius extremus* et *Nannopterygius enthekiodon*. *Macropterygius* sp. indet., avec des affinités de *Platypterygiinae*, autrefois dénommé *Ichthyosaurus trigonus*, est reconnu sur la base du matériel huméral. *Grendelius mordax* devient synonyme de *Brachypterygius extremus*. *Ophthalmosaurus monocharactus* devient synonyme d'*Ophthalmosaurus icenicus*. *Ichthyosaurus advena*, *Ichthyosaurus chalarodeirus* et *Ichthyosaurus hygrodeirus* sont rejetés comme *nomina nuda*. *Ichthyosaurus aequalis*, *Ichthyosaurus dilatatus*, *Ichthyosaurus ovalis*, *Ichthyosaurus thyreospondylus* et *Ichthyosaurus trigonus* sont rejetés comme *nomina dubia*. La plupart des restes proviennent des formations Oxford Clay et Kimmeridge Clay, mais on trouve du matériel d'ichtyosaure dans tout l'intervalle Aalénien–Portlandien.

Les affinités de *Baptanodon* sont envisagées, et il semble représenter une espèce d'*Ophthalmosaurus*, à savoir *Ophthalmosaurus natans*. Les caractères diagnostiques sont considérés importants au niveau de l'espèce seulement pour le séparer d'*Ophthalmosaurus icenicus*. La distribution paléogéographique d'*Ophthalmosauridae* suggère une origine au début du Jurassique moyen dans le sud-est de l'océan Pacifique, avec l'extension rapide de l'océan Téthys au Bathonien. [Translation by Yves Candela.]

Ichthyosaurier des britischen Mittel- und Oberjura.

ZUSAMMENFASSUNG

Das Material über Ichthyosaurier des britischen Mittel- bis Spätjura wird hier erneut aufgegriffen und beschrieben. Es gibt drei gültige Arten: *Ophthalmosaurus icenicus*, *Brachypterygius extremus* und *Nannopterygius enthekiodon*. *Macropterygius* sp. indet., das Ähnlichkeiten zu den Platypterygiinae aufweist und zuvor *Ichthyosaurus trigonus* genannt wurde, wird auf Basis von Oberarmknochenmaterial vermerkt. *Grendelius mordax* wird mit *Brachypterygius extremus* synonymisiert. *Ophthalmosaurus monocharactus* wird mit *Ophthalmosaurus icenicus* synonymisiert. *Ichthyosaurus advena*, *Ichthyosaurus chalarodeirus* und *Ichthyosaurus hygrodeirus* werden als *nomina nuda* abgelehnt. *Ichthyosaurus aequalis*, *Ichthyosaurus dilatatus*, *Ichthyosaurus ovalis*, *Ichthyosaurus thyreospondylus* und *Ichthyosaurus trigonus* werden als *nomina dubia* abgelehnt. Die große Mehrheit an Resten stammt aus den Oxford und Kimmeridge Tonerde Formationen, doch Ichthyosaurier werden in der gesamten Zeitspanne des Aalenium bis Portlandium gefunden.

Die Ähnlichkeiten bei *Baptanodon* werden berücksichtigt und es scheint, dass diese eine Art von *Ophthalmosaurus* darstellen: *Ophthalmosaurus natans*. Bestimmende Eigenschaften werden als wichtig erachtet, diese Art von *Ophthalmosaurus icenicus* ausschließlich auf der Spezies-Ebene abzugrenzen. Die paläobiogeografische Verteilung der Ophthalmosauridae lässt eine Herkunft aus dem südöstlichen pazifischen Ozean des frühen Mitteljuras, gefolgt von einer schnellen Ausbreitung gen Tethysmeer bis zum Bathonium vermuten. [Translation by David Schlaphorst.]

Ихтиозавры среднего и верхнего британского юрского периода.

РЕЗЮМЕ

В этой статье останки ихтиозавров Британского среднего и верхнего юрского периода пересматриваются и снова описываются. Появляются три валидные виды: *Ophthalmosaurus icenicus*, *Brachypterygius extremus* и *Nannopterygius enthekiodon*. *Macropterygius* sp. indet. (раньше названный *Ichthyosaurus trigonus*), что является подобным группе *Platypterygiinae*, замечается в связи с плечевым образцом. *Grendelius mordax* приравнивается к *Brachypterygius extremus*. *Ophthalmosaurus monocharactus* приравнивается к *Ophthalmosaurus icenicus*. *Ichthyosaurus advena*, *Ichthyosaurus chalarodeirus* и *Ichthyosaurus hygrodeirus* отвергаются в качестве *nomina nuda*. *Ichthyosaurus aequalis*, *Ichthyosaurus dilatatus*, *Ichthyosaurus ovalis*, *Ichthyosaurus thyreospondylus* и *Ichthyosaurus trigonus* отвергаются в качестве *nomina dubia*. Большинство останков происходит из формаций глины Оксфордского и Киммериджского яруса, но останки ихтиозавров находятся по целому Ааленскому–Портландскому ярусу.

Сходства рода *Baptanodon* рассматриваются и по-видимому является видом рода *Ophthalmosaurus*: *Ophthalmosaurus natans*. Определяющие характеристики считаются важными, чтобы различать его от *Ophthalmosaurus icenicus* только на уровне вида. Палеобиогеографическое распределение семейства *Ophthalmosauridae* указывает на происхождение на юго-востоке Мирового океана во время раннего среднего юрского периода, с последующим быстрым распространением на Тетис к Батскому ярусу.

[Translation by Anastasia Reynolds.]

ICHTHYOSAURS OF THE BRITISH MIDDLE AND UPPER JURASSIC.

PART 2. OTHER TAXA

Benjamin C. Moon and Angela M. Kirton

ABSTRACT

In Part 2, ichthyosaur taxa of the Late Jurassic are described; three taxa are considered valid: *Brachypterygius extremus*, *Nannopterygius enthekiodon*, and *Macropterygius* sp. indet. (Ichthyosauria: Ophthalmosauridae). These taxa are best represented from the Kimmeridge Clay Formation. *Grendelius mordax* is rejected as a junior subjective synonym of *Brachypterygius extremus* based on skull and limb morphology. Material referred to *Macropterygius* is too incomplete to erect a species, but is considered different enough to retain the genus as separate. *Ichthyosaurus aequalis*, *Ichthyosaurus dilatatus*, *Ichthyosaurus ovalis*, *Ichthyosaurus thyreospondylus*, and *Ichthyosaurus trigonus* are considered *nomina dubia*. *Ichthyosaurus advena*, *Ichthyosaurus chalarodeirus*, *Ichthyosaurus hygrodeirus*, and *Ichthyosaurus megalodeirus* are considered *nomina nuda*.

Comparisons are drawn with other ichthyosaur taxa, focusing particularly on Neoichthyosauria and Ophthalmosauridae. Evidence is presented for *Ophthalmosaurus* in the Kimmeridge Clay Formation, but the material is not complete enough to be certain of its specific affinities. *Ophthalmosaurus icenicus* and *Ophthalmosaurus natans* are considered separate species, but within the same genus based on several shared autapomorphies. However, re-evaluation of the material of *Ophthalmosaurus natans* is required.

Les ichtyosaures du jurassique moyen et supérieur britannique. 2ème Partie.

Brachypterygius, Nannopterygius, Macropterygius et Taxa invalida

RÉSUMÉ

Ichthyosaurier des britischen Mittel- und Oberjura. Zweiter Teil. *Brachypterygius*,

Nannopterygius, Macropterygius und Taxa invalida

ZUSAMMENFASSUNG

Ихтиозавры среднего и верхнего британского юрского периода. Часть вторая.

Brachypterygius, Nannopterygius, Macropterygius и Taxa invalida

РЕЗЮМЕ

ICHTHYOSAURS OF THE BRITISH MIDDLE AND UPPER JURASSIC.

PART 2. OTHER TAXA

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Genus *Brachypterygius* Huene, 1922b

Species *Brachypterygius extremus* (Boulenger, 1904)

Premaxilla

Maxilla

Nasal

Lachrymal

Prefrontal

Frontal

Parietal

Postfrontal

Supratemporal

Postorbital

Quadratojugal

Jugal

Orbit and sclerotic plates

Vomer

Pterygoid

Quadrate

Parabasisphenoid

Prootic

Opisthotic

Supraoccipital

Exoccipital

Basioccipital

Stapes

Dentary

Splénial

Surangular

Angular

Articular

Dentition

Vertebral column

Ribs

Clavicle

Coracoid

Scapula

Humerus

Forelimb epipodials

Carpals

Metacarpals

Primary forelimb digits

Accessory forelimb digits

Pelvic girdle and hindlimb

Genus *Nannopterygius* Huene, 1922b

Species *Nannopterygius enthekiodon* (Hulke, 1871)

Skull

Dentition

Vertebral column

Ribs

Coracoid

Scapula

Humerus

Forelimb epipodials and mesopodials

Pelvic girdle

Femur

Hindlimb epipodials and mesopodials

Genus *Macropterygius* Huene, 1922b

Humerus

TAXA INVALIDA

Genus *Ichthyosaurus* König, 1818

Ichthyosaurus advena Phillips, 1871

Ichthyosaurus aequalis Phillips, 1871

Ichthyosaurus chalarodeirus Seeley, 1869

Ichthyosaurus dilatatus Phillips, 1871

Ichthyosaurus hygrodeirus Seeley, 1869

Ichthyosaurus megalodeirus Seeley, 1869

Ichthyosaurus ovalis Phillips, 1871

Ichthyosaurus thyreospondylus Owen, 1840

Ichthyosaurus trigonus Owen, 1840

Genus *Ophthalmosaurus* Seeley, 1874b

Ophthalmosaurus monocharactus Appleby, 1956

Ophthalmosaurus pleydelli Lydekker, 1890

OSTEOLOGICAL COMPARISONS

DISCUSSION

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Genus BRACHYPTERYGIUS Huene, 1922b

Type species. Designated as *Ichthyosaurus extremus* by Boulenger 1904, p. 425; described from the Kimmeridge Clay Formation of Weymouth, Dorset, United Kingdom.

Other species. None.

Diagnosis. As for monotypic species below.

Etymology. The generic name *Brachypterygius* is derived from the Greek *βραχύς* ‘short’ and *πτέρυγα* ‘wing’, from the relatively short and broad holotype forelimb.

Discussion. Boulenger (1904) erected the species *Ichthyosaurus extremus* for the new specimen he described (NHMUK PV R3177). Huene (1922b) considered the configuration of the forelimb, particularly the distal humeral articulations, sufficient to place this species in the new genus *Brachypterygius*. As only the forelimb was known, little other material was referred to this taxon. With the finding of a new, large ichthyosaur skull from the Kimmeridge Clay Formation (CAMSM J68516), McGowan (1976) erected *Grendelius mordax*. He included a discussion on the validity of Upper Jurassic ichthyosaur taxa (excluding *Ophthalmosaurus*); *Brachypterygius extremus* was not discussed. Kirton (1983) re-described the material for both taxa, suggesting that the two genera might be synonymous (pp. 134–135), but refrained from a formal proposal as there was no overlapping diagnostic material. A new specimen, also from the Kimmeridge Clay Formation (BRSMG Ce 16696), of a largely complete ichthyosaur provided evidence to support Kirton’s view, and *Brachypterygius* and *Grendelius* were duly synonymized by McGowan (1997). Previous

research has regarded *Brachypterygius cantabrigiensis* (Lydekker, 1888) from the Cambridge Greensand Member (Albian, Lower Cretaceous) as a member of this genus (McGowan & Motani 2003), but a recent review of this material (Fischer *et al.* 2014a) considers this non-diagnostic. Remains from the Cretaceous Purbeck Limestone may be referable to *Brachypterygius*; however, the material is not certainly attributable to any genus (Delair 1968; Ensom *et al.* 2009).

Efimov (1998) named *Otschevia pseudoscythica* from the Tithonian of Russia. The partial forelimb included in the material differs from the holotype of *Brachypterygius* in having five digits instead of six. Few other differences are present, which led Maisch & Matzke (2000, p. 87) and McGowan & Motani (2003, p. 115) to consider *Otschevia* as a junior subjective synonym of *Brachypterygius*. Fernández (1997a, p. 752, fig. 1) referred specimen CMNH 47525 to *Brachypterygius* sp. based upon the small extracondylar area, large articular condyle that is not offset from the extracondylar area, poorly defined stapedial facets, and lack of basioccipital peg. These characters do not diagnose the specimen to genus or species level, and can be found in several Platypterygiinae-type ichthyosaurs, such as *Platypterygius* and *Sveltonectes* (Broili 1909; Fischer *et al.* 2011).

Zverkov *et al.* (2015) attempted to resurrect *Grendelius mordax* for CAMSM J68516 and BRSMG Ce 16696, and referred *Brachypterygius alekseevi* and *Brachypterygius zhuravlevi* to *Grendelius* also. Several characters used to diagnose *Grendelius* are inconsistent: exclusion of an intermedium-ulnare contact is present only in BRSMG Ce 16696 (Text-fig. 40c), not in the referred material of *Brachypterygius alekseevi* and *Brachypterygius zhuravlevi*. Variation in the size of elements between the right and left forelimbs in the holotype of *Brachypterygius alekseevi* (YKM 56702) means that the distal intermedium is pointed rather than flat, more similar in form to the *Brachypterygius extremus* holotype (NHMUK PV R3177). The distal humerus in BRSMG Ce 16696 and NHMUK PV

R3177 are both more anteroposteriorly elongate than the proximal humerus, whereas in the Russian material the proximal and distal humerus are similar sizes; this was used as a character in phylogenetic analyses. A concave dorsal lachrymal border is found in other Ophthalmosauridae (for example, see the description of *Ophthalmosaurus icenicus* in Part 1); a prominent hump on the nasal is not present in British material. The size difference between CAMSM J68516 and BRSMG Ce 16696 may be attributable to different ontogenetic stages, which is supported by the relatively different sizes of the eye (Fernández *et al.* 2005; Fischer *et al.* 2014). Further, ontogenetic and individual plasticity in the configuration of ichthyosaur limbs is widely reported (Motani 1999a; Maxwell 2012b; Maxwell *et al.* 2014). Here, we retain *Grendelius* as a junior subjective synonym of *Brachypterygius*, and refer CAMSM J68516 and BRSMG Ce 16696 to *Brachypterygius extremus*. We do not comment on the affinities of the Russian material, but leave the possibility of revision should further material become known.

The genus *Brachypterygius* may be characterized *in partim* by a premaxilla-jugal contact, three distal facets on the humerus, the middle of which is the smallest and articulates with the intermedium. This separates the humerus from *Ophthalmosaurus*, *Mollesaurus*, and *Undorosaurus*, also with three distal humeral facets, but the anterior facet is the smallest and articulates with a pre-axial accessory element. *Aegirosaurus* has the same distal humeral configuration as *Brachypterygius* and can be separated by having more elements in each digit (see diagnosis below), and a larger radial facet than the ulnar facet (Bardet & Fernández 2000; McGowan & Motani 2003). Similarly, *Maiaspondylus* also has the same configuration of distal humeral facets. The humerus of *Maiaspondylus* can be separated from *Brachypterygius* as the former taxon has equally expanded proximal and distal portions, whereas in *Brachypterygius*, the distal humerus is anteroposteriorly more expanded than the proximal humerus (Maxwell & Caldwell 2006). However, as the known material of

Maiaspondylus is juvenile, this may be a result of ontogenetic variation (Johnson 1979; Maxwell & Caldwell 2006).

Brachypterygius extremus (Boulenger, 1904) Pls 31–38; Text-figs 37–42

- v* 1904 *Ichthyosaurus extremus* Boulenger; p. 424, fig. 83 [Kimmeridge Clay Formation (Kimmeridgian Stage), Smallmouth Sands?, Weymouth, Dorset, UK].
- v . 1904a *Ichthyosaurus extremus* Boulenger; p. 18.
- v 1922b *Brachypterygius extremus* (Boulenger); von Huene, pp. 91, 97–98, pl. 19, fig. 9.
- 1934 *Brachypterygius extremus* Boulenger; Kuhn, p. 45.
- v 1959 *Macropterygius dilatatus* (Phillips); Delair, p. 65 [Kimmeridge Clay Formation (Kimmeridgian Stage), Swindon, UK].
- v 1976 *Grendelius mordax* McGowan; pp. 671–674, figs 1, 2A–C, F, 3 [Kimmeridge Clay Formation (Kimmeridgian Stage), Stowbridge, UK].
- 1982 *Grendelius mordax* Mc Gowan [*sic.*]; Mazin, p. 97.
- [v 1983 *Brachypterygius extremus* (Boulenger); Kirton, pp. 129–134, figs 40, 41.]
- [v 1983 *Grendelius mordax* McGowan; Kirton, pp. 110–121, figs 37, 38, pl. 4.]
- v 1985 *Brachypterygius extremus* (Boulenger); Delair, pp. 131–132, fig. 3 [Kimmeridge Clay Formation, Smallmouth Sands, UK].
- ? 1997a *Brachypterygius* sp. Huene; Fernández, p. 752, fig. 1 [Portlandian Stage, Ankilivalo, Madagascar].
- v 1997 *Brachypterygius extremus* (Boulenger); McGowan, p. 430, fig. 2A, B.
- ? 1998 *Brachypterygius zhuravlevi* Arkhangelsky; pp. 90–91, fig. 4 [*Dorsoplanites panderi* Zone (Volgian Stage), Krasnopartizanskaya District, Russia].
- v 1998 *Otschevia pseudoscythica* Efimov; p. 83, figs 1–4 [*Ilowaiskya pseudoscythica* Zone (Volgian Stage), Ulyanovsk Oblast, Russia].
- 1999b *Brachypterygius extremus* (Boulenger); Motani, p. 485.
- ? 2000 *Otschevia zhuravlevi* (Arkhangelsky); Arkhangelsky, p. 550, figs 1, 2 [*Dorsoplanites panderi* Zone (Volgian Stage), Krasnopartizanskaya District, Russia].

2000	<i>Brachypterygius extremus</i> (Boulenger); Maisch & Matzke, pp. 79–80, fig. 29 (<i>pars.</i>).
2003	<i>Brachypterygius extremus</i> (Boulenger); McGowan & Motani, p. 117, fig. 94, pl. 18.
2006	<i>Brachypterygius extremus</i> (Boulenger); Maxwell & Caldwell, pp. 1048–1050, fig. 6B (mod. Motani 1999b).
2010	<i>Brachypterygius extremus</i> (Boulenger); Maisch, p. 166.
.	2010 <i>Brachypterygius mordax</i> (McGowan); Maisch, p. 166.
v	2015 <i>Grendelius mordax</i> McGowan; Zverkov <i>et al.</i> , p. 562

Type material. Holotype: NHMUK PV R3177 (Text-fig. 42a), an embedded right forelimb designated by Boulenger (1904, p. 424, fig. 83c). This specimen comprises humerus, radius, ulna, radiale, ulnare, intermedium, and fifty-two other elements. Some of the forelimb elements were replaced in an unnatural position and are now held in plaster. The forelimb is exposed in dorsal view, and is currently on display in the Marine Reptiles Gallery of NHMUK. See the discussion below for locality and horizon.

Referred material. BRSMG Ce 16696 (Text-figs 38–40), a largely complete but only partially prepared specimen from Kimmeridge Bay, Dorset. The skull and right forelimb in ventral view and partial distal left forelimb are exposed.

Specimens in CAMSM: J29864 (Text-fig. 42b), a left forelimb, J61348, a basisphenoid, and J67556 (Text-fig. 42d, e; Pl. 33, figs 1–4), a right humerus, all from Ely, Cambridgeshire; J68516 and TN 571.11 (Text-figs 37, 41; Pl. 33), a large but poorly preserved skull with associated post cranial elements from Stowbridge, Norfolk; X39251 (Pls 31, 32, 34–37), a largely complete but disarticulated skeleton from Mepal, Cambridgeshire. (Many parts of X39251, but not all, are labelled with letter suffixes that are indicated in the descriptions below.) Additionally, part of this specimen is not ichthyosaurian.

Specimens in NHMUK (PV): R8693, pectoral girdle and forelimb elements from Encombe Bay, Dorset; 40337, a basisphenoid, and 41776, 45905 and 45907, basioccipitals, from Weymouth, Dorset; 42284, a right humerus, and 42286, a left humerus from the Isle of Portland, Dorset; 45984, a basioccipital and basisphenoid, 45986, a left articular, and 47326, a basisphenoid from Swindon, Wiltshire.

Specimens in OUMNH: J1585, a left humerus, J1586, a right humerus, J1608, left humerus, and J1627, a basioccipital, all from the ‘Portland Rock’ (Portland Stone Formation) of Swindon, Wiltshire; J68537, a basioccipital from an unknown horizon and locality; J68543, a basioccipital from Cumnor, Oxfordshire.

Specimen in WESTM: 1978.219 (Pl. 38, fig. 4), a left forelimb from Smallmouth Sands, near Weymouth, Dorset. This is possibly the contralateral forelimb to the holotype.

All of the above specimens are from the Kimmeridge Clay Formation unless noted (Table 5). The material is assigned based on the similarity with the type limb material – three distal humeral facets, large dorsal and ventral processes, polygonal limb elements – or in comparison with skull material of CAMSM J69516 and TN 571.11 – basioccipital with narrow extracondylar area and dorsally positioned notochordal pit; basisphenoid with well-offset basiptyergoid processes, ventrally positioned carotid foramen, and pentagonal form posteriorly.

Diagnosis. Moderately large to large (jaw length up to 1230 mm) member of Ophthalmosauridae characterized by: robust rostrum, snout ratio 0.567–0.905 (more gracile in *Ophthalmosaurus*, *Nannopterygius*, *Aegirosaurus*); premaxilla contacts jugal ventral to the external naris (autapomorphy); anterior tips of premaxillae and dentaries rounded (tapering and separate in *Ophthalmosaurus*); supranarial process of premaxilla extends over one-third of external naris (reduced in *Cryptopterygius*; does not contact jugal in *Ophthalmosaurus*,

Cryopterygius, *Maiaspondylus*, *Platypterygius*); dorsal rostrum squared in narial region (trapezoidal in *Ophthalmosaurus*); broad anterior jugal fan covering the maxilla and lachrymal laterally (narrower in *Ophthalmosaurus*, *Caypullisaurus*, *Platypterygius*); lachrymal contacts external naris (does not in *Cryopterygius*, *Platypterygius australis*); prefrontal excluded from contact with external naris by nasal and lachrymal (shared with *Cryopterygius*, *Ophthalmosaurus*, *Palvennia*, *Platypterygius*; contacts in *Aegirosaurus*); postorbital does not exclude quadratojugal in lateral view (shared with *Cryopterygius*, *Platypterygius*; quadratojugal excluded in *Aegirosaurus*, *Ophthalmosaurus*, *Palvennia*?); teeth relatively large (smaller in *Ophthalmosaurus*, *Aegirosaurus*, *Sveltonectes*); narrow postorbital region (wider in *Cryopterygius*, *Platypterygius*); basioccipital with narrow extracondylar area (broader in *Ophthalmosaurus*, *Mollesaurus*); notochordal pit on basioccipital condyle placed dorsally (central in *Ophthalmosaurus*); posterior border of coracoid straight and oblique (rounded in *Ophthalmosaurus*, *Acamptonectes*; transverse in *Cryopterygius*, *Platypterygius*); humerus with three distal facets, middle distal humeral facet is smallest and articulates with the intermedium (middle facet is largest and articulates with the radius in *Ophthalmosaurus*, *Caypullisaurus*, *Arthropterygius*); proximal elements of the accessory digits teardrop-shaped (rounded in *Ophthalmosaurus*, *Caypullisaurus*; polygonal in *Sveltonectes*, *Platypterygius*); anterior accessory element is positioned anterior to the radius and almost contacts the humerus proximally (shared with *Cryopterygius*; anterior accessory element positioned distal to the radius in *Aegirosaurus*; contacts the humerus in *Acamptonectes*, *Ophthalmosaurus*); five or six digits (six in *Ophthalmosaurus*); phalanges are rounded quadrangles (round in *Ophthalmosaurus*, *Arthropterygius*; polygonal in *Platypterygius*, *Sveltonectes*).

Etymology. The specific name *extremus* is Latin for ‘extreme’ or ‘broad’, most likely referring to the breadth or shortness of the holotype forelimb.

Occurrence. Material referable to *Brachypterygius extremus* is known from the Kimmeridgian–Tithonian of southern England. Further remains are known from France and Russia.

Discussion. The original notice of *Ichthyosaurus extremus* was given by Boulenger at a meeting of the Zoological Society of London. An abstract of this meeting (Boulenger 1904a) was published after an article in which Boulenger formally diagnosed *Ichthyosaurus extremus* (Boulenger 1904). Boulenger originally noted that the holotype’s (NHMUK PV R3177) horizon and locality were unknown (Boulenger 1904, p. 424). Mr Horace B. Woodward examined the matrix of the specimen and suggested it originated from the Lower Lias of Weston, near Bath, Somerset (Boulenger 1904, p. 426, 1904b). Andrews (1910, p. 54) noted the similarity between NHMUK PV R3177 and a humerus in the Passmore Collection (OUMNH J1608), suggesting that both likely derived from the same horizon: the Kimmeridge Clay Formation. This is strongly supported by a forelimb from the Kimmeridge Clay Formation of Weymouth (WESTM 1978.219) that may belong to the same individual as NHMUK PV R3177 (Text-fig. 42a; Pl. 38, fig. 4; Delair 1985, pl. 3). Following McGowan (1997) synonymizing *Grendelius* with *Brachypterygius*, he refrained from synonymizing *Brachypterygius mordax* with *Brachypterygius extremus* citing lack of preparation of specimen BRSMG Ce 16696, and a need for re-examination of the type material CAMSM J68516 and NHMUK PV R3177. McGowan & Motani (2003, p. 117) considered the differences in forelimb configuration (five digits versus six) to be of insufficient taxonomic value and synonymized *Brachypterygius mordax* with *Brachypterygius extremus*. However,

Maisch (2010) maintained *Brachypterygius mordax* as a separate species. Examination of the three specimens, NHMUK PV R3177, CAMSM J68516, and BRSMG Ce 16696, suggests that all belong to the same species, and therefore *Brachypterygius mordax* is considered a subjective junior synonym of *Brachypterygius extremus*.

Brachypterygius zhuravlevi Arkhangel'sky, 1998 was erected based on a partial forelimb, but it was later referred to *Otschevia zhuravlevi* (Arkhangel'sky 2000). The material referred to this taxon is consistent with *Brachypterygius pseudoscythica* and synonymized as suggested by Maisch & Matzke (2000, p. 79). McGowan & Motani (2003, p. 115) considered *Brachypterygius pseudoscythica* and *Brachypterygius zhuravlevi* to be subjective junior synonyms of *Brachypterygius extremus*. The brief descriptions of these taxa make detailed comparisons difficult, but the most obvious difference between *Brachypterygius pseudoscythica*, *Brachypterygius zhuravlevi*, and *Brachypterygius extremus* seems to be the number of elements in the forelimb (e.g. Efimov 1998, fig. 4). This feature is highly variable in other ichthyosaur taxa and is not considered to be diagnostic at the species level. Redescription of these taxa by Zverkov *et al.* (2015) has elucidated additional features (see also the generic discussion of *Brachypterygius* above), although the taxonomy between the taxa is still debatable; we therefore refrain from synonymising *Brachypterygius alekseevi* and *Brachypterygius zhuravlevi* with *Brachypterygius extremus*, as has been proposed by Maisch & Matzke (2000), McGowan & Motani (2003) and Maisch (2010). Some material previously referred to *Ichthyosaurus trigonus* (e.g. NHMUK PV 42284) is referable to *Brachypterygius extremus*. This taxon is considered a *nomen dubium* (see *Taxa invalida* below) and the original material and description did not include any diagnostic features; it is likely a collection of bones that may be referred to other taxa.

Description. Premaxilla. The premaxilla in *Brachypterygius extremus* is more robust than in *Ophthalmosaurus icenicus*, particularly anteriorly, but is otherwise largely similar in shape (Text-fig. 39; Table 6). Anteriorly, the tips of the two premaxillae are not separated: no tissue would have intervened as in *Ophthalmosaurus icenicus*. The tips also terminate more bluntly than in *Ophthalmosaurus icenicus*, which is particularly clear in CAMSM J68516, a result of the more robust build. This robustness was measured by the snout depth ratio as described by McGowan (1976, p. 676: $[10 \times \text{snout depth at midpoint}] \div \text{jaw length}$). For BRSMG Ce 16696, it is $(10 \times 45.9 \text{ mm})/810 \text{ mm} = 0.567$, and for CAMSM J68516, $(10 \times 111.3 \text{ mm})/1230 \text{ mm} = 0.905$ (Table 6). The considerable difference between these two results may be an effect of the crushing of CAMSM J68516. This is similar to McGowan's (1976) value; Kirton (1983) calculated the snout ratio for CAMSM J68516 as 0.80 and for *Ophthalmosaurus icenicus* as 0.65.

Laterally, a longitudinal groove becomes discontinuous anteriorly and opens into foramina that would likely have led to the internal part of the snout. Posteriorly, the premaxillae become more square dorsally than in *Ophthalmosaurus icenicus*, a character state that is continued posteriorly by the nasals (see below). The dorsal contact between the two premaxillae appears to be a simple butt joint. Posteriorly, the premaxilla meets and diverges around the external naris. The dorsal narial process appears to be small, smaller than the ventral process, in BRSMG Ce 16696, extending for about one-third of the external narial length, although this area is poorly preserved. The ventral process borders much of the ventral border of the external naris, meeting and overlapping the lachrymal posteriorly to exclude the maxilla from the external naris in lateral view. Fragments of the premaxilla are preserved in CAMSM X39251, but these offer no detail of the internal anatomy. The alveolar groove is present along the length of the premaxilla and holds about 28 teeth, similar to *Ophthalmosaurus icenicus*.

Maxilla. The maxilla is almost entirely covered by the premaxilla, lachrymal and jugal in lateral view (Text-fig. 39). Only the ventral portion is exposed and this extends along much of the ventral margin of the rostrum, further anteriorly than in *Ophthalmosaurus icenicus*. It is excluded from the border of the external naris in lateral view by the meeting of the premaxilla and lachrymal, and has a small contact with the overlying jugal also (see below). A fragment of maxilla is preserved in CAMSM X39251, but shows little detail; outwardly, the maxilla has the same form as in *Ophthalmosaurus icenicus*.

Nasal. The nasals are exposed for less than one-quarter of the pre-narial rostral length, and extend posteriorly dorsal to the orbit (Text-fig. 39). Dorsolaterally, they are square, which adds to the robust appearance of the snout. The nasals form the dorsal border of the external naris posterior to the dorsal narial process of the maxilla, and the margin of the nasal is smoothed and rounded along this border. As in *Ophthalmosaurus icenicus*, the posterior portion of the dorsal narial border is drawn laterally into a small, delicate triangular flange. This appears more strongly developed in CAMSM J68516, but the narial regions of this specimen and BRSMG Ce 16696 are heavily fragmented. The nasal meets the lachrymal at the posterior of the external naris and excludes the prefrontal from participating in the border of the external naris. The suture between the right and left nasals also seems to be a simple butt joint, as with the premaxilla (see above). There is no foramen, but an *excavatio internasalis* is present. Posteriorly, the nasals are deflected dorsally around the orbit and spread laterally to form a large part of the anterior portion of the skull roof. Here they are bordered by the prefrontal and postfrontal laterally and the frontals posteriorly, which they seem to underlap substantially.

Lachrymal. The lachrymal is well exposed in BRSMG Ce 16696, as the jugal and prefrontal, which overlap much of it, have been partly broken and removed (Text-fig. 39). It has the triradiate form seen in *Ophthalmosaurus icenicus*, but the main body is relatively larger anteroposteriorly, separating the external naris and orbit, and possibly creating a less elongate external naris. The anterior process forms a portion of the ventral margin of the external naris, meeting and underlapping the ventral narial process of the premaxilla anteriorly. Posteriorly, the dorsal process is overlapped by the narial process of the prefrontal, possibly excluding the prefrontal from the external naris. The posteroventral portion of the main body of the lachrymal is overlapped extensively by the jugal, although it is exposed dorsally and extends posteriorly along the dorsal margin of the jugal bar, forming the ventral margin of the orbit. The orbital process of the lachrymal extends for about one-half of the orbital length, longer than in *Ophthalmosaurus icenicus*, but in *Ophthalmosaurus icenicus* the anterior portion of the jugal does not cover the lachrymal. The supraorbital crest is present in *Brachypterygius extremus* and well developed, continuing onto the prefrontal dorsally. The posterior margin of the lachrymal is strongly smoothed and rounded to form the anterior orbital margin.

Prefrontal. Lateral crushing in BRSMG Ce 16696 has flattened the supraorbital crest of the prefrontal and it appears larger than it should (Text-fig. 39). As in *Ophthalmosaurus icenicus*, it forms a strong anterodorsal orbital margin between the lachrymal anteroventrally and the postfrontal posterodorsally. The lachrymal contact is broken ventrally, but there was significant overlap between the two elements. The prefrontal of CAMSM J68516 seems to be smaller than in BRSMG Ce 16696, and in *Ophthalmosaurus icenicus* (Kirton 1983); a result of the comparatively smaller orbit in CAMSM J68516. The posterior contact with the postfrontal is complex and interdigitating, with the postfrontal largely overlapping the

prefrontal dorsal to the midpoint of the orbit. The ventral surface of the prefrontal is broadened by the large supraorbital crest and is slightly concave both anteroposteriorly, following the orbit, and laterally. Dorsally, the nasal overlaps the prefrontal, but this contact cannot be seen clearly.

Frontal. The frontals are not well preserved in any available specimens of *Brachypterygius extremus*: their size is unknown in BRSMG Ce 16696 as they are still held within the matrix, and in CAMSM J68516 they are largely fragmentary (Kirton 1983).

Parietal. Specimen CAMSM X39251bj preserves most of the left parietal (Pl. 31, figs 1, 2), which has a similar form to the parietal of *Ophthalmosaurus icenicus*. The dorsal surface is smooth, and laterally convex anteriorly, descending laterally to form the medial wall of the supratemporal fenestra. The anterolateral portion is longitudinally grooved for articulation with the anteromedial portion of the postfrontal and the posterior portion of the frontal. Posteriorly, the medial portion of the dorsal parietal is concave. The medial surface is irregular and aligned sagittally to articulate with the contralateral parietal. Laterally, the posterior margin of the parietal is raised into low median flange, with an elongate concavity ventrally. The posterior of the parietal is deflected posterolaterally into a large process that articulates with the supratemporal; the posterolateral surface of this process is flattened. Ventrally, the surface of the parietal is incompletely prepared in CAMSM X39251. Anteriorly, the ventral surface is laterally concave, but posteriorly, it extends ventrally along the lateral and medial margins to form the broad supratemporal wall and parietal facet respectively.

Postfrontal. The postfrontal is a major part of the posterodorsal orbital margin and of the skull. The left postfrontal is well preserved in specimen CAMSM X39251ai (Pl. 31, figs 3, 4). This elongate, curved element forms the lateral border to the skull roof and the anterior and lateral borders to the supratemporal fenestra. It is largely similar to *Ophthalmosaurus icenicus*, but somewhat narrower in *Brachypterygius extremus*, reflecting the relatively smaller orbit. Anteriorly, the postfrontal is broad and flattened, and the dorsal surface is roughened where it would have been overlapped by the frontal medially. Posterior to this broad section, the postfrontal undergoes torsion as the posterior process becomes more dorsoventrally oriented. Medially, the margin of the postfrontal is strongly rounded and smooth as it forms the anterior and lateral margins to the supratemporal fenestra. The posterior portion of the postfrontal tapers posteriorly. Ventrally, this portion is ridged to separate it from the ventral surface of the postfrontal, which forms much of the dorsal surface of the orbital margin. This area is broadened by the development of the supraorbital flange laterally. A series of ridges and grooves anteriorly mark the contact with the prefrontal ventrally. At the anteromedialmost extent of the postfrontal contribution to the margin of the supratemporal fenestra, the postfrontal has a small facet, similar to that in *Ophthalmosaurus icenicus*, which may contact the parietal. The contact with the postorbital is not clear, but is extensive in BRSMG Ce 16696, forming an interdigitating contact along the ventral surface. The posterior part of the ventral surface of the postfrontal is ridged posteriorly, where it would have been underlapped by the anterior process of the supratemporal.

Supratemporal. A portion of the left supratemporal is present in CAMSM X39251bt (Pl. 31, figs 5, 6). This preserves much of the anterior and medial rami, reconstructed from several fragments; the ventral ramus has been broken. The anterior ramus extends anteriorly, curving slightly medially and tapering anteriorly. This ramus is oriented subvertically, with

longitudinal grooves and ridges on the external (lateral) surface that interlock with their counterparts on the internal surface of the postfrontal (see above); the extent of this contact is marked by a low ridge. The dorsomedial margin of the anterior ramus is smoothed and rounded to form the posterolateral margin to the supratemporal fenestra, continuing posteriorly from the postfrontal. The internal surface appears slightly roughened, probably for muscle attachment, as suggested in *Ophthalmosaurus icenicus* above. Posterior to this facet, the three rami meet and the posterolateral apex of the supratemporal is drawn into a slight tubercle, not as well developed as in some specimens of *Ophthalmosaurus icenicus*. The bone surface is roughened for attachment of muscle slips. The medial ramus is a robust spur of bone that would meet the posterolateral process of the parietal. The parietal facet is large, oblique, and triangular, situated at the distal end of the medial ramus of the supratemporal, but incomplete ventrally. In the middle of the posterior face is a small shelf of bone that may mark the dorsalmost portion of the opisthotic facet, as in *Ophthalmosaurus icenicus*. However, this area, and much of the ventral ramus, is poorly preserved.

Postorbital. The postorbital is a narrow, subtriangular element that forms much of the posterior border of the orbit; it is not well known in *Brachypterygius* (Text-fig. 39). Dorsally, the postorbital contacts the ventral postfrontal and extends ventrally to contact and cover the dorsal process of the jugal laterally. The postorbital is similar in form to that of *Ophthalmosaurus icenicus*, including a small portion of the supraorbital flange developed dorsally in BRSMG Ce 16696. The postorbital in BRSMG Ce 16696 is broken, but is associated with another element that is interpreted as the quadratojugal (see below).

Quadratojugal. The quadratojugal is largely exposed in BRSMG Ce 16696 (Text-fig. 39). It is a subtriangular bone in the lateral cheek region. The quadrate facet and the posterior

corner of the quadratojugal is broken posterodorsally. Specimen CAMSM X39251 preserves a more complete example of what is interpreted as the left quadratojugal (Pl. 31, figs 7, 8). This shows a similar form to that of *Ophthalmosaurus icenicus*, although it is proportionally larger. The facets for contact with the surrounding bones are less distinct than in *Ophthalmosaurus icenicus*, being surrounded by smaller ridges. The facets for the postorbital and squamosal also appear narrower than those in *Ophthalmosaurus icenicus*, however, they are not well preserved in CAMSM X39251. Kirton (1983) inferred the presence of a quadratojugal in CAMSM J68516 with a pointed-elliptical cross-section and a small section of the curved anterodorsal margin. This specimen shows the jugal overlying the quadratojugal, although this probably arose from displacement.

Jugal. The jugal is present in BRSMG Ce 16696 and forms a long J-shaped bar ventral to the orbit (Text-fig. 39). It covers much of the lateral maxilla anteriorly; the dorsal portion may cover much of the lachrymal as well, but is broken. At its anteriormost tip, the jugal contacts the posterior of the subnarial process of the premaxilla, excluding the maxilla from external contact with the external naris. Therefore, anteriorly, the jugal is broader than in *Ophthalmosaurus icenicus*. The main part of the horizontal bar is curved ventral to the orbit, widening and becoming shallower posteriorly. This forms a shelf ventral to the orbit with a distinct dorsal ridge that may mark attachment for muscles. A rounded heel is developed at the posteroventral corner of the jugal, as in *Ophthalmosaurus icenicus*. The dorsal margin is curved dorsally where the jugal is developed into a dorsal process; the extent of this is not known as it is covered by the quadratojugal.

Orbit and sclerotic plates. Specimen BRSMG Ce 16696 appears to preserve a complete sclerotic ring, although this is fragmented and the sutures between the plates are difficult to

determine (Text-fig. 39); several complete and fragmented sclerotic plates are preserved with CAMSM X39251 (Pl. 32, figs 8–11). It is likely that there are about 14 sclerotic plates in total, about the same as in *Ophthalmosaurus icenicus*. Although they have been crushed, they still show evidence of the convex curvature that is also found in *Ophthalmosaurus icenicus*. The orbit itself is much smaller than in *Ophthalmosaurus icenicus*. McGowan's (1976) orbital ratio gives values of $215 \text{ mm}/1230 \text{ mm} = 0.174$ in CAMSM J68516, and $147.6 \text{ mm}/810 \text{ mm} = 0.182$ in BRSMG Ce 16696 (compare with *Ophthalmosaurus icenicus*, NHMUK PV R3013: 0.28; Table 6).

Vomer. Portions of the right and left vomers are preserved in CAMSM X39251; both represent the near-posterior raised portion that formed the medial choanal walls (Pl. 32, figs 1, 2). The vomer is raised dorsally into a sagittally-aligned, anteroposteriorly convex, but dorsoventrally concave dorsal sheet. The dorsal part of this has subparallel dorsoventral ridges along the surface, and is pierced by foramina. Anterodorsally, the base of a process is preserved that may have been similar to the more elongate processes in *Ophthalmosaurus icenicus*. Ventrally on this surface, on the anterior part of the region preserved, is a larger foramen that traverses the vomer posteromedially to the medial surface. As in the vomer of *Ophthalmosaurus icenicus*, this portion of the vomer is interpreted as the medial choanal wall. Ventrally, the vomer broadens to form a larger basal plate. The anterior part of the lateral surface of the basal plate is formed into a long, triangular facet that articulates with the palatine. Posterior to this facet, the basal portion of the vomer becomes lower and is pierced by anteroventrally–posterodorsally elongate foramina. At the posterior end of the preserved portion, the ventrolateral surface of the vomer is irregular: a longitudinal groove is surrounded dorsally and ventrally by uneven ridges that separate it from the choanal wall dorsally, and the ventral surface. Only the ventral portion of the medial surface of the vomer

is well preserved. There is a channel that becomes dorsoventrally narrower posteriorly, interpreted as the pterygoid facet. The surface of this facet is pierced by foramina from the lateral surface. The ventral surface of the vomer is a flattened, smooth surface that narrows anteriorly, and is broad to the posterior end of the preserved portion.

Pterygoid. Much of the posterior part of the pterygoid is exposed in ventral view in BRSMG Ce 16696 (Text-fig. 39; Pl. 32, figs 3, 4) and has a similar form to that of *Ophthalmosaurus icenicus*. This bone is emarginated posteriorly, separating the palatal and quadrate rami. The lateral wing is exposed and is shorter and broader than in *Ophthalmosaurus icenicus*; the distal margin is well rounded and has a slight rugosity, suggesting that it would have held muscle or ligament attachments. At the anterior of the pterygoid, the suture with the palatine may be present, but this is uncertain. The pterygoid is the best represented palatal element in CAMSM X39251bh, but only the posterior portion of the right pterygoid is preserved (Pl. 32, figs 3, 4). This has three posterior flanges, dorsal, lateral, and medial, that articulate with the quadrate (dorsal and lateral flanges) and with the basisphenoid medially, but the specimen has been dorsoventrally crushed. The lateral margin is rounded and the pterygoid expands laterally towards its posterior end. There is a large dorsolateral concavity to accept the pterygoid lamella of the quadrate between the lateral and dorsal flanges. Ventrally, the surface of the pterygoid is smoother than the dorsal surface and becomes concave posteriorly between the lateral and medial flanges. Medially at the posterior end, is a large tuberos growth that likely indicates pathology.

Quadrate. Specimens CAMSM X39251ab and X39251aq preserve a complete right quadrate and the ventral portion of the left quadrate respectively (Table 6; Pl. 32, figs 5–7). The form of this element is largely indistinguishable from certain examples of

Ophthalmosaurus icenicus, forming the characteristic C-shape. The pterygoid lamella is a slightly roughened plane of bone to which the supratemporal dorsally, and the pterygoid ventrally, would have been applied. Central on this face, a small excavation marks the facet for the stapes, although it is poorly defined in this specimen. The dorsal and medial margins of the quadrate are emarginated and would have been continued in cartilage. At the ventral part of the medial margin, the quadrate forms a heel, as the margin is deflected laterally towards the articular condyle. The internal surface is convex dorsoventrally and laterally, and smooth, forming part of the posterior wall of the adductor chamber. The lateral margin is emarginated, with the dorsal portion drawn slightly anteriorly; the quadratojugal would have articulated across this emargination. The ventral articular boss is rather worn, but also seems to have two articular facets, as in *Ophthalmosaurus icenicus*: an anterolateral facet for the glenoid fossa of the surangular, and a posterolateral facet for the articular. Both of these are irregularly pitted, indicating the presence of cartilage in life.

Parabasisphenoid. The parabasisphenoid of *Brachypterygius extremus* is not known completely: the parasphenoid is co-ossified with the base of the basisphenoid, as in *Ophthalmosaurus icenicus*, but is frequently broken off and lost (Text-fig. 41c; Pl. 33, figs 1–4, Pl. 34, figs 1–4). This description therefore will focus on the basisphenoid (posterior) portion. Although broadly similar in form to that of *Ophthalmosaurus icenicus*, there are key diagnostic differences between the two taxa.

The anterior face of the basisphenoid is trapezoidal as in *Ophthalmosaurus icenicus*. Many of the anterior features seen in *Ophthalmosaurus icenicus* are not as clear in *Brachypterygius extremus*, particularly the development of the *dorsum sellae* and the anterior articulations of the trabecular cartilages, but this may be an effect of preservation. Between the facets for the trabecular cartilage, the pituitary fossa is much reduced in *Brachypterygius*

extremus compared to *Ophthalmosaurus icenicus*. There are no foramina located lateral to this in *Brachypterygius extremus* either. The ventral portion of the anterior face is strongly swollen medially, as the posterior part of the parasphenoid is more robust and deeper than in *Ophthalmosaurus icenicus*. In dorsal view, the anterior face is not as clearly visible as it is in *Ophthalmosaurus icenicus*, and the dorsal articulations for the stapes and basioccipital appear to extend to the anterior edge of the basisphenoid. In this view, and particularly in ventral view, the basipterygoid processes can be seen, and are clearly more substantial and wing-like than in *Ophthalmosaurus icenicus*. The posterior dorsal surface is dominated by the heavily pitted facets for stapes and basioccipital, with cartilaginous intervention. A dorsoventral groove is also present, as in *Ophthalmosaurus icenicus*. The ventral view shows the differences from the basisphenoid of *Ophthalmosaurus icenicus* most clearly. The basipterygoid processes are clearly separated from the main body of the basisphenoid and noticeably angled anteriorly. Distally, they are somewhat anteroposteriorly shorter and more rounded than the broad, square processes in *Ophthalmosaurus icenicus*, but would have been covered in cartilage. Posteriorly, the basipterygoid processes are bordered by a deep groove that Kirton (1983) suggested transmitted the palatine nerve. Ventrally, the single internal carotid foramen is placed further posteriorly in *Brachypterygius extremus* than in *Ophthalmosaurus icenicus*, to meet the posterior portion of the parasphenoid at its posteriormost point, rather than surrounding it laterally. The suture between parasphenoid and basisphenoid ventrally is clearly visible in CAMSM X39251ae, and the parasphenoid does not contact the internal carotid foramen. However, in CAMSM TN 571.11 (= J68516), the parasphenoid may form a small shelf ventral to the internal carotid foramen. The posterior margin of the basisphenoid in *Brachypterygius extremus* is angled laterally around the basioccipital and stapediaal facets so that the whole element has a more pentagonal shape in ventral view than in *Ophthalmosaurus icenicus*.

Prootic. A partially preserved prootic is present in CAMSM X39251ce (Pl. 34, figs 5, 6); which side of the skull it originates from cannot be determined certainly, but it is tentatively treated as a right prootic based on the criteria outlined by Kirton (1983). The external (anterior) surface is heavily worn, and only the lateral and medial margins remain. In internal (posterior) view, there are smooth-floored impressions of the membranous labyrinth in the middle of the prootic, forming a V-shape that swells medially and ventrally. The medial portion of these impressions has a further depression medially, and there is a smaller pit ventrally; these may indicate the positions of the sacculus and utriculus respectively (see also the prootic of *Ophthalmosaurus icenicus* above). The margins of the posterior prootic are rounded and roughened for the cartilage that surrounded the otic capsule.

Opisthotic. Both opisthotics are present in CAMSM X39251ap (left) and X39251as (right), but the right opisthotic is the best preserved (Pl. 34, figs 7–12). The massive medial body is squared in anterior and posterior views, with a short, robust paroccipital process that extends dorsolaterally. The anterior surface is smooth and concave laterally along the paroccipital process, but medially is ridged to separate from a large anteroventrally facing facet, which articulates with the dorsal stapes. Dorsal to the ridge is a narrow groove that traverses dorsolaterally towards the paroccipital process. The dorsal surface of the opisthotic is smooth and concave, but rounded convexly towards the posterior surface. Medially, the opisthotic has two main parts: the more anterodorsal portion faces medially and shows the V- or T-shaped impressions of the membranous labyrinth. This is surrounded by a narrow articular surface on most sides, apart from posteroventrally, where there is a larger articulation as the opisthotic meets the exoccipital medially. The ventral surface is roughened for articulation with the basioccipital and the stapes ventrally. The basioccipital portion is

represented anteromedially by a slight upturning of the facet, while the major part is given to the stapedial facet posteriorly. The stapedial facet is divided by a posteriorly-positioned, laterally directed groove.

Supraoccipital. The supraoccipital is preserved in CAMSM X39251bt and forms a squared arch in anterior and posterior views (Pl. 35, figs 1–4). The dorsal margin of the supraoccipital is thickened and grooved as it was continued anterodorsally by cartilage. In dorsal and ventral views, the supraoccipital has a C-shape: laterally the supraoccipital is continued anteriorly by two large processes. On the anterolateral surfaces of these processes, there are T-shaped impressions that mark the passage of the membranous labyrinth anteriorly. Dorsal to these impressions, the supraoccipital broadens to meet the dorsal margin, but there is a shallow groove that separates the more anterior section dorsal to the otic capsule. The internal face of the supraoccipital is smooth and is pierced on the lateral surfaces by two foramen that traverse to near the lateral margins of external posterior surface. The posterior surface is smooth in its ventral portion, and separated from the anterolateral otic surface by a rounded, thickened ridge ventrolaterally. Two small concavities are present on the ventrolateral part of the posterior surface, and face posterolaterally. The dorsal portion of the posterior surface is roughened and raised dorsal to the lateral surfaces by a broad ridge, which traverses dorsolaterally. The supraoccipital portion of the *foramen magnum* is large, over one-half of the height of the supraoccipital, and is squared dorsally. There is no median ventral process on the roof of the *foramen magnum*, as in *Ophthalmosaurus icenicus*. There is a ventral constriction of the supraoccipital portion of the *foramen magnum* between the ventral exoccipital articulations laterally, but this is not as strong as in *Ophthalmosaurus icenicus*. Ventrally, there are two small, triangular facets that articulate with the dorsal

exoccipitals. These facets are concave and broadest posteriorly, and the points of the facets are aligned subparallel towards the anterior.

Exoccipital. The exoccipitals are essentially identical in both *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. They form a short column between the basioccipital ventrally and the supraoccipital dorsally, enclosing the *foramen magnum* (Table 6). The anterior face is largely smooth, but pierced by a large foramen medially. Dorsally, the surface is pitted for the application of cartilage and slopes ventrally, posterolaterally forming a ridge that encloses part of the vagus foramen, completed laterally by the opisthotic. The ventral surface is drawn out anteriorly into a long, broadly triangular, tapering tongue. This surface is also pitted for cartilage and is convex to fit the concave exoccipital facets of the basioccipital (see below). In *Brachypterygius extremus*, there are three foramina on the anterolateral face, compared to two in *Ophthalmosaurus icenicus*. Maisch (1997a) has described exoccipitals from *Ophthalmosaurus icenicus* with three lateral foramina, so this feature may be variable (see *Exoccipital* in the description of *Ophthalmosaurus icenicus* above).

Basioccipital. The basioccipital of *Brachypterygius extremus* is also different from that of *Ophthalmosaurus icenicus* (Text-fig. 41a, b; Table 7; Pl. 33, figs 5–8). It forms the entirety of the articulation with the vertebral column as a hemispherical boss, but anteriorly is not as broad. The anterior face is subpentagonal and heavily pitted for the cartilage that intervened between this face and the posterodorsal face of the basisphenoid; the corresponding median groove is also present. This groove traverses the entire anterior face of the basioccipital in *Brachypterygius extremus*, precluding the presence of a basioccipital peg, or the rudiments thereof. There are no specimens that show the smoothing associated with the structures of the otic capsule that is found in some specimens of *Ophthalmosaurus icenicus*. Dorsally, the

basioccipital has two lateral concavities into which the ventral face of the exoccipitals fit, with cartilage intervening. Between these, the grooved, smooth-based ridge forms the floor of the *foramen magnum*, not raised as high as in *Ophthalmosaurus icenicus*. The exoccipital facets are more triangular than in some specimens of *Ophthalmosaurus icenicus*. This may be a result of variable ossification, or indicate that the exoccipital may have been applied more closely to the basioccipital in *Brachypterygius extremus*.

Much of the lateral surface of the basioccipital is taken up by facets for the opisthotic, dorsally, and stapes, ventrally. The opisthotic facet is poorly defined, not as obvious as in *Ophthalmosaurus icenicus*, but takes the form of a broad pitted boss on the dorsal anterolateral part of the basioccipital. Ventral to this, the stapedial facet is separated from the opisthotic facet by a low, obliquely-angled ridge. The oval stapedial facet itself seems to be concave, as it is formed of two contacts, separated by a median ridge, anterior to a strong dorsoventral ridge. This last ridge separates the stapedial facet from the extracondylar area posteriorly. The extracondylar area in *Brachypterygius extremus* is much narrower than in *Ophthalmosaurus icenicus*, forming only a limited dorsoventral strip around the anterior of the condyle articulation. The resulting difference in form between *Brachypterygius extremus* and *Ophthalmosaurus icenicus* is most clearly seen in posterior view: the extracondylar area is barely visible in the former, compared to the broad concavities that are seen in the latter. Ventrally, the basioccipital of *Brachypterygius extremus* is not developed into large tubera, confluent with the extracondylar area, as in *Ophthalmosaurus icenicus*. Together, these differences give the basioccipital of *Brachypterygius extremus* a smaller, more rectangular appearance than that of *Ophthalmosaurus icenicus*. The basioccipital condyle in *Brachypterygius extremus* is not clearly separated from the extracondylar area. This surface is rugose for the application of the articular cartilage. A small notochordal pit is placed dorsally

on the condyle, more dorsally than in *Ophthalmosaurus icenicus*, and may be dorsoventrally elongated.

Stapes. A poorly preserved stapes is associated with the right pterygoid in CAMSM X39251bh (Pl. 32, fig. 3). It appears similar to the stapes in *Ophthalmosaurus icenicus*, with a massive medial boss and more slender lateral shaft, but is smaller relative to the size of the pterygoid. No other examples of the stapes in *Brachypterygius extremus* are known.

Dentary. The dentary extends along much of the lower jaw, as in *Ophthalmosaurus icenicus*, and, like the premaxilla (see above), is somewhat more robust in *Brachypterygius extremus* (Text-figs 37, 39). Its posterior extent is uncertain, although it is likely to have extended to a similar position as in *Ophthalmosaurus icenicus*: approximately ventral to the orbital midpoint. The anterior tip of the dentary is rounded, like the premaxilla and unlike the tapering anterior tip found in *Ophthalmosaurus icenicus*; the nature of the symphysis is uncertain. McGowan's (1976) jaw depth ratio is $46.1 \text{ mm}/810 \text{ mm} = 0.569$ for BRSMG Ce 16696, $77 \text{ mm}/1230 \text{ mm} = 0.626$ in CAMSM J68516 (compared to 0.72 in McGowan 1976), and 0.47 in *Ophthalmosaurus icenicus* (Kirton 1983). For much of the pre-orbital length of the dentary, a longitudinal groove is present, discontinuous anteriorly, leading to several foramina that are directed internally, as is the case in the premaxilla and in *Ophthalmosaurus icenicus*. The posterior portion of this groove widens dorsoventrally into a more distinct channel that shallows towards the posterior dentary. This is unlike *Ophthalmosaurus icenicus* in which the groove tends to taper posteriorly. Ventrally, the dentary meets the splenial, excluding the splenial from lateral exposure ventrally for about the anterior one-third of the lower jaw. Posterior to this, the angulars intervene between the dentary and splenial, excluding the latter from lateral view. The posterior portion of the dentary tapers dorsally,

exposing the main body of the surangular ventrally. The alveolar groove is present along much of the length of the dentary. In BRSMG Ce 16696, the dentary holds at least 36 teeth, while in CAMSM J68516, there are about 51 teeth in the dentary.

Splenial. A small part of the splenials is exposed ventrally in BRSMG Ce 16696 and fragments are preserved in CAMSM X39251 (Text-fig. 39). These are too poorly exposed or preserved for description, but they appear to be similar to those of *Ophthalmosaurus icenicus*. The ventral margin of the splenial is well rounded where it takes part in the ventral margin of the mandible and the lateral face has a low ridge into which the ventromesial portion of the angular fits.

Surangular. The surangular has a moderate exposure in the lateral mandible; its contact with the dentary is oblique and long dorsally, and it is covered extensively by the angular ventrally (Text-figs 37, 39). Both surangulars are well preserved in CAMSM X39251y, X39251aa, X39251ak, and X39251cf (Pl. 36, figs 1–8). The anterior ramus of the surangular is narrow at the anterior end where it is covered laterally by the dentary and medially by the splenial, but becomes dorsoventrally higher posteriorly, forming a vertical sheet. The articulation with the dentary is marked laterally by a posteroventrally-directed ridge dorsal to the Meckelian canal in the middle of the surangular. Dorsally, the margin of the surangular is rounded and the lateral surface just ventral to this margin is smooth. At about the midpoint of the surangular, there is a low rise in the dorsal margin. In its posterior region, the surangular becomes broader, and a second ridge traverses from the middle of the lateral surface posterodorsally towards the posterior end. The medial surface is concave dorsoventrally. Anteriorly, there is a longitudinal ridge along the midline that may mark the articulation with the splenial medially. Posterior to this ridge, the surangular is less well-preserved, but has a

series of longitudinal ridges posteriorly. The posterior ends of the surangular are present, and similar to *Ophthalmosaurus icenicus*. The dorsal margin is raised into a long process, the paracoronoid process, anterior to a dorsally-facing, bowl-like concavity. Medially, there is a large, dorsomedially-deflected process for attachment of the *M. adductor mandibulae externus* group, which is anterior to another anteroposterior concavity that marks the jaw glenoid articulation. The posterolateral surface of the surangular is rounded posteriorly and roughened, while the medial surface is rougher still for articulation with the articular.

Angular. The angular has significant exposure along the posterior mandible in BRSMG Ce 16696, greater than the surangular exposure, but unlike in *Ophthalmosaurus icenicus*, although this may be a result of crushing of the skull (Text-figs 37, 39; Pl. 35, figs 5, 6). The posterior angular curves gently dorsally, and the external surface is convex, meeting the splenial ventrally. The angular inserts between the dentary and the splenial, and is covered internally by the latter. The partial left angular in CAMSM X39251 is rod-like anteriorly, with a convex, rounded, triangular ventral margin, and two longitudinal grooves dorsally. These hold the ventral surangular (lateral groove) and form the floor of the Meckelian canal (medial groove) respectively. The grooves are separated by a sharp ridge that migrates posterolaterally, and becomes less distinct. Towards the posterior of the mandible, the angular gradually becomes higher, bordering the surangular dorsally. The grooves end abruptly at this dorsal deflection of the dorsal angular surface. The posterior angular fans over the surface of the mandible, ventral to the jaw articulation, and is covered by radiating striations, likely marking the attachment of cartilage. This cartilage would continue posterior to the articulation forming a short retroarticular process.

Prearticular. Specimen CAMSM X39251cb is interpreted as the posterior portion of the prearticular (Pl. 36, figs 9, 10). The prearticular is a thin vertical sheet that articulates between the surangular laterally and the splenial medially in its anterior region, but is medially exposed in its posterior portion. Laterally, the prearticular is flat, with a roughened surface for articulation. The middle portion of specimen CAMSM X39251cb is raised into a high, rounded, sheet-like process, which is interpreted as ventral to the paracoronoid process based on comparison with *Ophthalmosaurus icenicus* (see *Prearticular* in the description of *Ophthalmosaurus icenicus* and Text-fig. 17 in Part 1). The medial surface of the anterior part of this specimen is smooth and slightly convex dorsoventrally. Posteriorly, the prearticular is deflected medially as the dorsal process descends, as well as the posteriormost portion of the specimen; the dorsal margin is grooved medially posterior to the process. Ventrally, a groove ascends on the lateral surface of the prearticular to the posterior end of the preserved portion; the surface ventral to this is roughened.

Articular. A few specimens of articulars have been referred to *Brachypterygius extremus* (or its synonyms). Only the articular with CAMSM X39251ar is certainly from this taxon (Pl. 35, figs 7, 8), but others (e.g. NHMUK PV 45986) are also likely referable to *Brachypterygius extremus*. The articular is small and rounded, as in *Ophthalmosaurus icenicus*, but can be more extensive dorsolaterally, as in NHMUK PV 45986 and apparently BRSMG Ce 16696. Its anterior surface is dominated by the dorsal facet for the articular condyle of the quadrate (see above), a large, oval, rugose area directed anteriorly and slightly dorsally. Ventral to this, there may be another smaller facet developed (CAMSM X39251ar) directed anteroventrally to articulate with possibly the angular or prearticular; this facet is not found in *Ophthalmosaurus icenicus*. However, this may also be a constriction between the articular facet dorsally and angular facet ventrally. The angular facet is placed in the middle

of the ventral margin of the articular, which is slightly drawn out ventrally as a shallow concavity. Medially, the surface of the articular is shaped like a shallow saddle, weakly concave anteroposteriorly, but strongly convex dorsoventrally. Posterior to the anterior articular facet, a slightly roughened, rounded ridge descends ventrally towards the main body. The posterior portion of the articular is rounded and roughened, suggesting a cartilaginous covering. Laterally, the surface is planar, but strongly ridged and grooved longitudinally, likely complementary to the medial surface of the surangular, to form a strong contact to the jaw.

Dentition. The teeth of *Brachypterygius extremus* are similar in form to those of *Ophthalmosaurus icenicus*, but noticeably larger relative to the jaw size (Text-figs 37, 39; Pl. 37, figs 1–9). Unlike *Ophthalmosaurus icenicus*, teeth have been found with all substantial jaw remains of *Brachypterygius extremus*, which allows for more accurate tooth counts. Specimen BRSMG Ce 16696 preserves 50 teeth in the upper jaw, of which 23 are in the maxilla, and at least 35 in the lower jaw; specimen CAMSM J68516 has 53 teeth in the upper jaw, 23 in the maxilla, and slightly more than 51 in the lower jaw; numerous disarticulated teeth are preserved with CAMSM X39251. These values are comparable to *Ophthalmosaurus icenicus* (see *Dentition* of *Ophthalmosaurus icenicus* above), in which there are around 50 teeth in each jaw, with 23 in the maxilla also.

The largest teeth are towards the middle of the jaw, as in *Ophthalmosaurus icenicus*: the largest exposed tooth in CAMSM J68516 is over 47 mm high apicobasally (Kirton 1983: 53.4 mm), with a 24.2 mm high crown, but missing the tooth root; incomplete teeth in CAMSM X39251 are 69.45 mm and 72.30 mm in apicobasal height. Tooth size decreases towards the anterior and posterior ends of the alveolar groove, but not to the extent seen in *Ophthalmosaurus icenicus*. This continuously robust dentition may be one cause for the lack

of anterior tapering of the premaxillae and dentaries, and the rounded snout otherwise seen in *Ophthalmosaurus icenicus*. McGowan's (1976) tooth index ($10 \times$ crown height of largest tooth/jaw length) is $16.2 \text{ mm}/810 \text{ mm} = 0.200$ for BRSMG Ce 16696, and $24.2 \text{ mm}/1230 \text{ mm} = 0.197$ for CAMSM J68516. This value is the same as found by Kirton (1983), but much lower than the 0.37 of McGowan (1976). The alveolar groove is not well exposed in the two specimens described above, but fragments of the jaw in CAMSM X39251 have the low partial septa forming impressions where the teeth would sit (aulacodont dentition of Mazin 1983 and Motani 1997).

Each tooth is curved slightly lingually, but not to the same extent as in *Ophthalmosaurus icenicus*. The tooth crowns are conical, longitudinally striated, and comprise about one-third of the tooth height with a well-defined enamel base. Immediately basal to the tooth crown, the root is smooth. The tooth bases of the largest teeth are bulbous, sub-quadrangular, and smooth. A resorption pit is present lingually on the base of the tooth where developing teeth would lie before erupting. In smaller teeth, such as CAMSM X39251c, the crown comprises a larger portion of the tooth height, the root is also more bulbous and rounded, with no apparent root ornamentation basally, or resorption pit lingually. This specimen likely represents a posterior maxillary tooth.

Vertebral column. Vertebrae are preserved disarticulated and out of sequence in CAMSM J68516, so that it is difficult to be sure of trends along the vertebral column. Several vertebrae are found *in situ* in BRSMG Ce 16696, but these have not been prepared completely, which prevents a detailed description. Kirton (1983) noted that the vertebrae are relatively larger in *Brachypterygius extremus* than in *Ophthalmosaurus icenicus*: 90.5 mm high (CAMSM J68516) compared to 75.3 mm (NHMUK PV R4753). They are amphicoelous and take the typical ichthyosaurian form of short discs. However, rather than the near-circular

cross section found in *Ophthalmosaurus icenicus*, in *Brachypterygius extremus* the ventral margins of the anterior to middle presacral centra appear to be slightly parabolic in anterior and posterior views. Dorsally, the base of the neural canal is a roughened, square area that sits between the two raised pedestals of the neural arch facets laterally. These are slightly concave to receive the pedicels of the neural arches. Laterally, the surfaces of the centra are anteroposteriorly concave and pierced by nutritive foramina: less frequent and larger than in *Ophthalmosaurus icenicus*. The rib facets are separated into diapophysis and parapophysis in many of the vertebral centra; the same divisions are used as in *Ophthalmosaurus icenicus* (see *Vertebral column* of *Ophthalmosaurus icenicus* in Part 1). In one centrum where the diapophysis is closest to the neural arch facet, but clearly separate, the rib facet is entirely detached from the anterior margin of the centrum. In *Ophthalmosaurus icenicus*, these would be connected by a thin, poorly ossified, cartilaginous ridge. Those centra with single rib facets, interpreted as belonging to the caudal region, are similar to those of *Ophthalmosaurus icenicus*, but are not as strongly square ventrally, retaining a slight curve. Ventral thickening for articulation with haemal arches could not be confirmed.

Five anterior neural spines are preserved, but poorly exposed, in left lateral view in BRSMG Ce 16696, possibly on the anteriormost five vertebrae (Text-fig. 40). These increase greatly in height posteriorly, approximately doubling in height from first to last; the last is a little higher than its centrum, although the outlines cannot be seen clearly. The lower part appears to form a short pedestal, presumably creating the neural arch, slightly facing anteriorly and articulating with the posterior portion of the preceding neural arch at about one-third of its height. Dorsally, the neural spine is directed posterodorsally and broadens anteroposteriorly. Distally, the neural spine articulates with the anterior and posterior spines.

Ribs. Fragments of ribs are preserved in specimen CAMSM X39251, but are poorly exposed in BRSMG Ce 16696 (Text-fig. 40). These appear similar to those of *Ophthalmosaurus icenicus*, but the distal shape is unknown. Proximal fragments, and facets on the vertebral centra, show bicipital articulations with the centra along at least some of the axial skeleton, probably becoming unicipital in the caudal series.

Clavicle. The clavicles are preserved in CAMSM X39251ag and X39251aj (Pl. 37, figs 10–13). These are elongate and curved dorsolaterally towards the distal ends. They are not as robust as in *Ophthalmosaurus icenicus*. The external (anterior) surface is convex dorsoventrally. The medial margins of both clavicles are incomplete, so the nature of the articulation between the two is uncertain. The medial portion is oriented transversely, but at about one-half of its length laterally, the clavicle is deflected dorsolaterally, creating a heel on the posterior margin; distally, the clavicle tapers to a point. Posteriorly, the clavicle is grooved medially to receive the anterior interclavicle. The groove is more distinct just lateral to the medial clavicle, and becomes shallower distally. Ventral to this groove, the margin of the clavicle is drawn posterior to hold the interclavicle, but not to the same extent as in *Ophthalmosaurus icenicus*. The posterior surface of the distal clavicle is roughened. The distalmost tips of two clavicles are poorly preserved.

Coracoid. Two incomplete coracoids are present in CAMSM J68516 and a (right?) coracoid is exposed in ventral view in BRSMG Ce 16996 (Text-fig. 40). The coracoids appear to be relatively longer and narrower in *Brachypterygius extremus* than in *Ophthalmosaurus icenicus*. A single anterior notch is present laterally. The coracoids are saddle-shaped, with the lateral margins raised to accommodate the lateral articular surfaces. The lateral facet does not seem as large as the medial facet. From CAMSM J68516, the

coracoids appear more equidimensional than in BRSMG Ce 16696, likely following posterior breakage in the former specimen. The posterior border in BRSMG Ce 16696 is partially exposed and is straight, separated from the lateral facet by an obtuse angle. This is quite different from regularly rounded posterior margins seen in the coracoids of *Ophthalmosaurus icenicus*.

Scapula. Separate proximal and distal regions of the scapula are partially exposed in BRSMG Ce 16696, and a proximal right scapular fragment and nearly complete left scapula are present in CAMSM X39251 (Text-fig. 40; Pl. 37, figs 14, 15). The form of the scapula is similar to *Ophthalmosaurus icenicus*, with a ventrally expanded proximal portion and a narrower, strap-like distal portion. The proximal articular margin is pitted, like in *Ophthalmosaurus icenicus*, but not as strongly curved in *Brachypterygius extremus* as in *Ophthalmosaurus icenicus*, forming a less strong S-shape proximally, although the lateral surface is strongly concave. The borders of the proximal facets on the scapula are difficult to determine in CAMSM X39251, but it is likely that there are two main articulations, dorsally and ventrally, for the glenoid and coracoid respectively. A groove along the proximal margin suggests cartilage was present. Posteroventrally, the scapula is expanded laterally into the teardrop-shaped coracoid articulation. The dorsal margin of the scapula is raised proximally to form a concave area between the dorsal margin and the coracoid facet ventrally. In CAMSM X39251, this is not well developed and, although there is evidence of a distinct acromion process, this is not as large as in some specimens of *Ophthalmosaurus icenicus*, and is not offset from the main body of the scapula. Distally, the scapula forms a thin, wide shaft that is curved medially and broadens distally. The ventral margin of the scapula is strongly concave while the dorsal margin is nearly straight, only becoming slightly concave proximally. Medially, the proximal scapula is concave between the raised dorsal margin and

ventrally expanded portion posterior to the coracoid articulation; this concavity extends along one-half of the scapular length in CAMSM X39251 as the marginal ridges reduce posteriorly.

Humerus. Several humeri are referable to *Brachypterygius extremus*, including the holotype (NHMUK PV R3177), a probable counterpart (WESTM 1978.219), and BRSMG Ce 16696 (Text-figs 40, 42; Tables 8, 9; Pl. 38). The last of these allows establishment of the synonymy of *Brachypterygius extremus* and *Grendelius mordax* (see *Discussion* of the genus above). The holotype is crushed and broken proximally, and BRSMG Ce 16696 is only visible in ventral view, but WESTM 1978.219 is largely complete, although it has some minor crushing, and can be taken out of its mount and viewed from all angles.

The humerus broadly takes a similar form to that of *Ophthalmosaurus icenicus*, but with some differences that are of taxonomic importance. It is a short, robust element with a large and rounded proximal head, constricted diaphysis, and greatly expands anteroposteriorly towards the distal end to accommodate three distal humeral facets. The proximal surface is gently convex and heavily pitted for a large amount of cartilage that would intervene between this and the glenoid formed by the scapula and coracoid (see above). As in *Ophthalmosaurus icenicus*, the proximal surface is broadened dorsoventrally by the development of large dorsal and ventral processes, to which strong muscles would have attached. The uncrushed specimen CAMSM J67556 shows that the angle across these processes is slightly less than in *Ophthalmosaurus icenicus*, about 30° relative to the anteroposterior axis, as the ventral deltopectoral crest is not as anteriorly developed in *Brachypterygius extremus* as in *Ophthalmosaurus icenicus*. The dorsal process is strongly developed into a high, plate-like ridge that extends distally and slightly anteriorly from the proximal surface of the humerus for about one-half of the humeral length. It is confluent with the proximal surface of the humerus and much of the dorsal margin of this ridge is also pitted, but not as much as the

proximal articular surface, becoming smoother distally and descending to the main body of the humerus. In specimen CAMSM J67556, the proximal margin of the dorsal ridge is slightly excavated into a low channel. This process is surrounded by large concavities anteriorly and posteriorly. The deltopectoral crest is not as well demarcated as the dorsal process, forming a large triangular expansion proximally, with an anteriorly placed proximodistal ridge. This ridge decreases in prominence distally, extending for about one-half of the humeral length. These dorsal and ventral expansions give the humerus a triangular cross section proximally, and a broad surface in anterior view. As in *Ophthalmosaurus icenicus*, this causes the anterior edge of the diaphysis to be more round than the posterior edge, aiding in orientating specimens.

Distally, the humerus expands anteroposteriorly to at least the width of the proximal portion, usually slightly greater. The anterior part is drawn anteriorly slightly relative to the posterior part, leading to a slight asymmetry across the middle facet and the long axis of the humerus in dorsal view. This is well shown in NHMUK PV R3177 and WESTM 1978.219, and results in a more acute angle at the anterodistal extremity than at the posterodistal. In cross section, the distal shape contrasts with that of the diaphysis: anteriorly pointed and posteriorly round, which is the case in *Ophthalmosaurus icenicus*. The distal face is divided into three facets by low ridges, which articulate with (anterior to posterior) the radius, intermedium (the smallest), and ulna. Between each facet, a large obtuse angle is visible in dorsal or ventral view, so that the radial, intermedial, and ulnar facets are directed anterodistally, distally, and posterodistally respectively. The radial and ulnar facets are approximately the same size, but anterior extension of the distal humerus can make the radial facet larger. In specimen WESTM 1978.219, the humerus is drawn anteriorly enough that it may have articulated with the proximal part of the anterior accessory element: a poorly-developed potential facet is present. The distal margin of the radial facet may also be

concave. Between these, the intermedial facet is smaller, and allows a clear distinction between this taxon and *Ophthalmosaurus icenicus*: in the latter, the anterior facet is the smallest, and the middle facet is the largest. Compared to the holotype (NHMUK PV R3177), specimen CAMSM J29864 has a narrower intermedial facet. Kirton (1983) attributed this feature to more advanced ossification in the holotype, however, this is unlikely as both specimens are large and well ossified. The surface of these distal facets is concave to accept the epipodials and intermedium, and slightly rugose, indicating that cartilage intervened between the facets and more distal elements.

Forelimb epipodials. The radius and ulna articulate with the anterior and posterior distal facets of the humerus (see above; Text-figs 38, 40c, 42; Pl. 38, fig. 4). They are of similar size, although the ulna is consistently slightly larger than the radius in the specimens examined. The radius and ulna are both subquadrate, thickened elements, becoming thicker towards the midline of the forelimb. The dorsal and ventral surfaces are roughened, while the other surfaces are deeply and irregularly pitted where the articular cartilage would have been applied. Both the radius and ulna usually articulate distally with three elements each. The radius articulates with (anticlockwise from anterior) the proximal element of the anterior accessory digit, radiale, and intermedium, while the ulna articulates with the intermedium, ulnare, and proximal element of the posterior accessory digit. In some specimens (i.e. BRSMG Ce 16696 and WESTM 1978.219), there can be a small, but not close, articulation with one of the median proximal carpals. The radius is almost entirely surrounded by the humerus and distal forelimb elements; its articular faces are all unfinished. The proximoposterior portion of the ulna is free and here the ulna thins and the posterior edge is thin and slightly concave.

Carpals. There are three proximal carpals and four distal carpals in *Brachypterygius extremus* (after Motani 1999a), but these have been displaced when compared to *Ophthalmosaurus icenicus* by the expansion and more proximal position of the intermedium, and are therefore not aligned in the same manner (Text-figs 40, 42; Pl. 38, fig. 4). The radiale and ulnare are thickened elements, similar to the radius and ulna proximally, and quadrate or pentagonal in outline. Distally, they articulate with two elements of the distal carpal row and one or two accessory digit elements each. The elements are also pitted on their articular faces as cartilage intervened. Unlike in *Ophthalmosaurus icenicus*, the radiale and ulnare may not have a contact with the intermedium medially, and, if present, this is often very small. There is no contact between the radiale and intermedium in specimen WESTM 1978.219, nor between the intermedium and ulnare in BRSMG Ce 16696. If WESTM 1978.219 is the contralateral forelimb to NHMUK PV R3177, this shows that contact between these elements is variable.

The intermedium in *Brachypterygius extremus* is greatly expanded in comparison to *Ophthalmosaurus icenicus*: it is larger than the other proximal carpals and larger than the radius, matching the size of the ulna. It is also located more proximally than in *Ophthalmosaurus icenicus* to articulate with the humerus. To accommodate this placement, the intermedium is subhexagonal in shape, with a flattened proximal margin and a pointed distal margin. The intermedium is thicker than the other proximal carpals, matching the epipodials. The intermedium articulates with (clockwise from proximal in the right forelimb, NHMUK PV R3177; Text-fig. 40c) the humerus, radius, variably radiale, distal carpals three and four, ulnare, and ulna. The radiale and ulnare facets are the smallest. In specimen BRSMG Ce 16696, the distal margin of the intermedium is flattened rather than pointed. This is because distal carpal three, and digit three, are positioned more posteriorly, along the midline of the forelimb, than in other specimens, which could be a result of the comparatively

poorly-developed posterior accessory digit (see below). Much variation is found in the shape of the intermedium between specimens assigned to this taxon, and therefore this difference is not considered to be taxonomically important.

Three distal carpals are present, and their identification follows the system applied to *Ophthalmosaurus icenicus* above, and the work of Kirton (1983) and Motani (1999a), representing elements 2–4 of the pentadactyl limb (Text-fig. 40c). The distal carpals, along with the more distal rows, are not aligned: element two is displaced slightly distally relative to the other two. These elements are more regularly polygonal than the equivalent elements in *Ophthalmosaurus icenicus*. The median two elements are broadly pentagonal as they articulate with the distal facets of the intermedium, whereas the more marginal elements are quadrate. Distal carpal two has a small notch in the middle of both the proximal and distal margins, best seen in specimen WESTM 1978.219, like many of the more distal elements, which is roughened and may mark the attachment point of ligaments that bind the limb elements.

Metacarpals. The four metacarpals each articulate with one distal carpal proximally. Metacarpal five is shifted proximally and essentially replaces distal carpal five (after Motani 1999a; Text-figs 40, 42; Pl. 38, fig. 4). The metacarpals are similarly polygonal, unlike the more clearly rounded metacarpals of *Ophthalmosaurus icenicus*. The metacarpals and phalanges are more closely positioned to each other in *Brachypterygius extremus* than in *Ophthalmosaurus icenicus*, with less cartilage intervening. In the holotype, NHMUK PV R3177, metacarpals three and four are fused along the midline, but with the suture still visible. Kirton (1983) suggested that this indicated little movement at this point in the forelimb, but the cause may be pathological (Maxwell 2012b). The metacarpals also have notches in the proximal and distal margins.

Primary forelimb digits. The distal elements in the forelimb of *Brachypterygius extremus* are arranged in straight longitudinal columns, parallel to the proximodistal long axis of the forelimb (Text-figs 40, 42; Pl. 38, fig. 4). This is different to the condition in *Ophthalmosaurus icenicus*, where the proximal metapodial columns are aligned slightly anterodistally, while the more distal elements are aligned more closely to the long axis of the forelimb, creating an apparent anterior curve in the digits. In *Brachypterygius extremus*, there are four primary digits, supported by the four metacarpals proximally, as is the case in *Ophthalmosaurus icenicus*. However, in BRSMG Ce 16696, the reduced ulnare, proximal carpal four, and metacarpal five reduce the width of the forelimb in the second row of limb elements (Text-fig. 40). The holotype (NHMUK PV R3177) and WESTM 1978.219 both have eight phalanges preserved in each digit; the discoidal shape of the distalmost elements suggest these digits are complete. The other specimens, CAMSM J29864 and BRSMG Ce 16696, have much longer forelimbs, with 16 elements in the latter specimen. This disparity in phalangeal number could be diagnostic to separate the specimens into two species. However, considering other consistencies between the specimens, in the forelimb and the rest of the skeleton, and the variability exhibited by ichthyosaur limbs generally (shown in *Mixosaurus cornalianus* and *Stenopterygius* spp.: Maxwell 2012b, tables 1–4), we still consider both configurations to be representative of *Brachypterygius extremus*. As the holotype is partially reconstructed, and thus incomplete, it may be that this specimen and WESTM 1978.219 do not possess their true number of phalanges. The history of these specimens is not recorded, so it is difficult to be certain.

The proximal phalanges in *Brachypterygius extremus* are also clearly quadrangular, closely spaced and anteroposteriorly elongate, whereas in *Ophthalmosaurus icenicus* they are rounded, spread out, and sub-equidimensional. These proximal elements have a median notch

in the proximal and distal margins, like the carpals and metacarpals proximally. This notch, which is not found in *Ophthalmosaurus icenicus*, may be developed as the elements are closely spaced, with less cartilage intervening. It would allow the digits to be held rigidly in their parallel columns. A single additional ossicle is present between the first and second phalanges of digits three and four of BRSMG Ce 16696. The phalanges gradually thin and decrease in size distally, with a sudden large decrease from the level of the third phalanx in the holotype that might be due to reconstruction (Kirton 1983). In WESTM 1978.219, the phalanges do not greatly decrease in size until more distally (around phalanx five). This sudden decrease is not seen as clearly in BRSMG Ce 16696, and any size decrease distally is more gradual as it is spread over more elements. Distally, the phalanges become more rounded and discoidal, particularly the two distalmost elements.

Accessory forelimb digits. *Brachypterygius extremus* possesses two accessory digits, located at the anterior and posterior margins of the forelimb that extend for more than one-half the length of the distal forelimb (Text-figs 40, 42; Pl. 38, fig. 4). The most proximal element in each digit is narrow and teardrop-shaped with a pointed proximal apex and broad distal bulge. In cross section, these elements are wedge-shaped, strongly narrowing towards the margins of the forelimb. This shape, coupled with the thicker median elements gives the forelimb a streamlined shape, as seen in numerous other ichthyosaurs (McGowan 1992). In the anterior accessory digit, the proximal element articulates with the radius and radiale, while the proximal element in the posterior digit articulates with the ulna and ulnare. The close relationship of these elements to the humerus might suggest contact between the humerus and the cartilaginous portion of the accessory element. Where this comes closest, in WESTM 1978.219, there may even be the rudiments of an additional distal facet on the humerus (see above). The more distal accessory elements are similar in form to the elements

of the primary digits, although consistently more rounded and slightly smaller. Distally, they shrink and become discoidal, as in the primary digits. The accessory digits in *Brachypterygius extremus* are more substantial than in *Ophthalmosaurus icenicus*, extending for 11 elements in both NHMUK PV R3177 and BRSMG Ce 16696. Associated with the posterior accessory digit, between and posterior to elements three and four, is an additional ossicle; similar ossicles may be found in *Ophthalmosaurus icenicus* and other ichthyosaur taxa.

Pelvic girdle and hindlimb. No portion of the pelvic girdle or hindlimb is known from British material of *Brachypterygius extremus*, although elements are potentially preserved in part of the unprepared portion of BRSMG Ce 16696.

Genus NANNOPTERYGIUS Huene, 1922b

Type species. Designated as *Ichthyosaurus enthekiodon* by Hulke (1871, p. 441) from the Kimmeridge Clay Formation of Kimmeridge Bay, Kimmeridge, United Kingdom.

Diagnosis. As for monotypic species.

Etymology. The generic name *Nannopterygius* is derived from Greek *νανος* ‘dwarf’ and *πτέρυγα* ‘wing’, from the extremely reduced paddles.

Discussion. Hulke (1870) described some fragmentary remains from the Kimmeridge Clay Formation of Kimmeridge Bay, Dorset, UK, collected by Mr J. C. Mansell. He placed these in the new genus *Enthekiodon* Hulke, 1870, but did not erect a species, noting that they

were similar to *Ichthyosaurus*. The name *Enthekiodon* refers to the apparent insertion of the teeth into low cups formed by upgrowths of the jaw around the tooth base (Hulke 1870). This likely refers to the low septa found in some jaw specimens, and not indication of non-aulacodonty. The location of Hulke's (1870) material is unknown. The following year, Hulke (1871) named *Ichthyosaurus enthekiodon* from a largely complete specimen from the same horizon and locality. As he considered the material to be the same as *Enthekiodon*, Hulke (1871) demoted this nomen to specific level within the genus *Ichthyosaurus*: *Ichthyosaurus enthekiodon*. Huene (1922b) erected *Nannopterygius* to receive this species.

Nannopterygius enthekiodon (Hulke, 1871) Pl. 39, figs 1–5; Text-figs 43, 44

- ? 1870 *Enthekiodon* Hulke; p. 174 [no specific name given] [Kimmeridge Clay Formation (Kimmeridgian Stage), Kimmeridge Bay, Kimmeridge, UK].
- *v 1871 *Ichthyosaurus enthekiodon* Hulke; pl. 17 [Kimmeridge Clay Formation (Kimmeridgian Stage), Kimmeridge Bay, Kimmeridge, UK].
- v 1889 *Ichthyosaurus entheciodon* Hulke; Lydekker, p. 32, figs. 3?, 16 [unjustified emendation] [Kimmeridge Clay Formation (Kimmeridgian Stage), Weymouth, UK].
- 1902b *Ichthyosaurus entheciodon* Hulke; Sauvage, p. 402.
- 1911 *Ichthyosaurus entheciodon* Hulke; Sauvage, p. 442 [Upper Kimmeridgian, Boulonnais, France].
- v 1922b *Nannopterygius entheciodon* (Hulke); Huene, pp. 91, 98, pl. 12, fig. 2 [cop. Hulke, 1871].
- 1923 *Nannopterygius euthecodon* [sic.] (Hulke); Huene, p. 467.
- 1976 *Nannopterygius enthekiodon* (Hulke); McGowan, p. 671.
- 1982 ?*Nannopterygius enthekiodon* (Hulke); Mazin, p. 91.
- [v 1983 *Nannopterygius enthekiodon* (Hulke); Kirton, pp. 122–128, fig. 39, pl. 5.]
- ? 1985 *Nannopterygius enthekiodon* (Hulke); Delair, p. 133, fig. 9.
- 1992 *Nannopterygius entheckiodon* [sic.] (Hulke); Bardet, p. 654.
- 1999b *Nannopterygius enthekiodon* (Hulke); Motani, p. 484.

- 2000 *Nannopterygius enthekiodon* (Hulke); Maisch & Matzke, p. 81.
- v 2003 *Nannopterygius enthekiodon* (Hulke); McGowan & Motani, p. 109, fig. 91 [cop. Hulke 1871].
- 2010 *Nannopterygius enthekiodon* (Hulke); Maisch, p. 167.

Type material. Holotype: NHMUK PV 46497, a largely complete, but poorly preserved embedded skeleton designated by Hulke (1871, p. 441, pl. 17), from the Kimmeridge Clay Formation of Kimmeridge Bay, Kimmeridge, Dorset, UK. It is currently on display in the Marine Reptiles Gallery of NHMUK. The specimen possesses an almost complete, but disrupted skull, much of the vertebral column and ribcage is present, the coracoids and fragments of the scapula and clavicles as well as proximal portions of both forelimbs and a partial hindlimb.

Referred material. The following material was assigned to this species by Lydekker (1889): NHMUK PV 46497a, a partial right hindlimb (Lydekker 1889, p. 33; Pl. 39, figs 1–5) from the same locality and horizon as the holotype; R1197, a partial skeleton with caudal vertebral centra, pelvis, and left forelimb from Chapman’s Pool, Dorset, and 46473e, a series of 35 vertebral centra from Foxhangers, Wiltshire (figured by Owen 1881, pl. 22); all are from the Kimmeridge Clay Formation. From the Oxford Clay Formation, Lydekker included NHMUK PV 47424, a femur from Peterborough, Cambridgeshire, and R5832, three cervical vertebrae, is from the Oxford Clay Formation of Fletton, Cambridgeshire (Pl. 39, figs 6–8) was referred subsequently (Table 10). None of this material is diagnostic.

Delair (1985, p. 133) identified new specimens (SOTUG 15181, 15198, 15348, 16566, and 16663) from the Kimmeridge Clay of Rope Lake Head, Dorset, as *Ophthalmosaurus* (Table 10). While none of these remains are truly diagnostic, the coracoids figured (Delair 1985, p. 133, fig. 9) are similar to those in the holotype of *Nannopterygius enthekiodon*:

elongate, straight intercoracoidal facet, posterolaterally angled posterior margin: this likely represents a new occurrence for this taxon. The whereabouts of these specimens is currently unknown. Possibly related specimens are known from the Tithonian lithographic limestones of Solnhofen, Germany (Frickhinger 1994; Bardet & Fernández 2000).

Diagnosis. Moderately large (jaw length 600 mm, estimated 3000 mm total length) member of Ophthalmosauridae characterized by: gracile rostrum (less robust than in *Brachypterygius* and relatively longer than in *Cryptopterygius*); orbital ratio 0.22 (lower than in *Ophthalmosaurus*, *Palvennia*; larger than in *Brachypterygius*, *Cryptopterygius*); teeth rather small, with fine enamel ridges; 42 presacral vertebrae (42 in *Ophthalmosaurus*; 47 in *Platypterygius australis*); relatively large vertebral centra in the sacral region (higher and longer than in *Ophthalmosaurus*); ribs with single groove proximally (shared with *Acamptonectes*); strongly reduced pectoral girdle and forelimb (autapomorphic); coracoids elongate, aspect ratio 1.67, with large, square anteromedial process (sub-equidimensional, 1.06, and rounded in *Ophthalmosaurus*, *Acamptonectes*; smaller anteromedial process in *Cryptopterygius*); two distal humeral facets (three in *Ophthalmosaurus*, *Acamptonectes*, *Aegirosaurus*, *Caypullisaurus*, *Undorosaurus*, *Brachypterygius*, *Arthropterygius*); metapodials rounded (polygonal in *Platypterygius*, *Sveltonectes*, *Caypullisaurus*); two distal femoral facets (three in *Platypterygius americanus*, *Platypterygius australis*, *Platypterygius hercynicus*).

Etymology. The specific name *enthekiodon* derives from the Greek ἐνθετα ‘insert’, κούττα ‘cup’ and δόντια ‘teeth’, from the supposed implantation of the teeth in the jaw.

Occurrence. Kimmeridgian, Upper Jurassic of southern England, United Kingdom.

Discussion. This taxon is poorly known, resulting mostly from a lack of referable material. Most specimens assigned to *Nannopterygius enthekiodon* are vertebrae that cannot be distinguished from many other ophthalmosaurids, or Jurassic ichthyosaurs more generally. The holotype specimen (NHMUK PV 46497) is currently on display in the Marine Reptiles Gallery at the NHMUK and is inaccessible for detailed study. As of writing (mid-2015), plans are afoot to make this specimen available. Further specimens from England and France have been referred to *Nannopterygius enthekiodon* by Lydekker (1889) and Sauvage (1911), none of which shows diagnostic features (see above; Kirton 1983). A partial skeleton from the Tithonian Solnhofen Limestone Formation of south-western Germany was referred to this taxon by Frickhinger (1994), however, this has not been fully described and its affinities are uncertain.

Nannopterygius enthekiodon was included in Ophthalmosauridae (= Ophthalmosauria) by Motani (1999b, p. 484) due to its similarity with *Ophthalmosaurus*, but has not formally been included in a phylogenetic analysis. Huene (1922b, p. 98) mentioned the similarity of the skull to *Ophthalmosaurus*: long snout, large orbit, and short postorbital segment. Synapomorphies of Ophthalmosauridae recovered in the most recent phylogenetic analysis (Fischer *et al.* 2013) cannot easily be applied to *Nannopterygius enthekiodon* due to the incomplete preservation of the material. Several characters suggest that *Nannopterygius enthekiodon* should be included within this clade: (1) postorbital skull $< \frac{1}{3}$ the length of the orbit diameter (Jiang *et al.* 2005, character 7; this character is homoplasious and shared with mixosaurids); (2) posterior dorsal vertebrae $< 3.5\times$ higher than long (Fischer *et al.* 2013, character 60; this character is non-homoplasious); (3) equally-sized proximal and distal humeral anteroposterior lengths: this is a synapomorphy of Ophthalmosauridae recovered by Fischer *et al.* (2013, characters 40) under DELTRAN optimisation; (4) humerus with

posteriorly deflected ulna facet (Fischer *et al.* 2013, character 42) is shared by *Ophthalmosaurus icenicus* + *Acamptonectes densus* clade; (5) femur with prominent dorsal and ventral processes (Fischer *et al.* 2013, character 60), this character is an unambiguous and non-homoplasious synapomorphy of Fischer *et al.*'s (2013) *Ophthalmosaurus icenicus* + *Platypterygius hercynicus* clade within Ophthalmosauridae. While several of these characters are ambiguous and/or homoplasious, these together suggest that *Nannopterygius enthekiodon* is likely an ophthalmosaurid ichthyosaur, however, a full phylogenetic analysis is required to confirm this.

Description. Skull. The skull is poorly preserved and crushed resulting in the sutures between bones being difficult to distinguish (Text-fig. 43). The premaxillae and dentary are broken towards their anterior ends, but the length of the jaw can be measured at about 600 mm. These elements are lightly built as in *Ophthalmosaurus icenicus*, and slender, not as robust as in *Brachypterygius extremus*, and they taper slightly towards the anterior end. The narial region has largely been lost. Posterior to this, the orbit can be discerned, but the bones surrounding it, and sclerotic plates, are heavily fractured. The orbit is not as large in *Nannopterygius enthekiodon* (McGowan's 1976 orbital ratio: 130 mm/600 mm = 0.217), relative to skull size, as it is in *Ophthalmosaurus icenicus* (NHMUK PV R3013: 0.28), but is larger than in *Brachypterygius extremus* (CAMSM J68516: 0.174, BRSMG Ce 16696: 0.182). Small parts of the jugal, lachrymal, postorbital, and postfrontal(?) can be determined around the orbit. These have been disturbed (Kirton 1983): the postorbital has moved anteriorly and the anterior part of the jugal slightly dorsally. The posterior part of the skull is also heavily fractured and partly obscured by the vertebral column posteriorly. A small part of the posterior of the lower jaws remains intact, but the outlines of the bones cannot be observed; it seems similar to the configuration in *Ophthalmosaurus icenicus*.

Dentition. The first remains that Hulke (1870) assigned to *Enthekiodon* were teeth, and he described them at length. This description focuses on the bulbous tooth bases, a character found in all the Upper Jurassic taxa and many from the Lower Jurassic and Cretaceous (Kirton 1983; McGowan & Motani 2003). None of the 15 teeth preserved in NHMUK PV 46497 is complete. The largest crown preserved is 8.8 mm high, implying a tooth index (McGowan 1976) of $(10 \times 8.8 \text{ mm})/600 \text{ mm} = 0.147$. This is slightly larger than in *Ophthalmosaurus icenicus* (0.140), but smaller than in *Brachypterygius extremus* (0.197, 0.200). The crowns are slender cones, longitudinally ridged, with a well-defined enamel base. More basally, the root is bulbous and appears rounded, although it may be slightly quadrangular, and is formed largely of cementum.

Vertebral column. The holotype specimen has about 65 vertebrae preserved, mostly visible in approximately right lateral view (Text-fig. 43). The division between the presacral and caudal regions (see *Vertebral column* in the description of *Ophthalmosaurus icenicus* in Part 1) are in similar positions to *Ophthalmosaurus icenicus*: around the 42nd vertebra, although Hulke (1871) determined the 45th. In the anterior centra, the rib facets are bicipital, with the diapophysis confluent with the neural arch facet dorsally. These gradually separate, but where this occurs is uncertain, perhaps around centrum 20–25, and the rib facets move ventrally, becoming closer. The two rib facets meet at centrum 42, marking the presacral–caudal split, and the single facet gradually becomes more rounded posteriorly in the column.

Preservation in the holotype allows little to be seen of the vertebrae and few measurements can be taken, but they appear to be similar to those of *Ophthalmosaurus icenicus*. Generally, the height of the centra increases posteriorly along the presacral portion of the column, reaching the greatest height around the 42nd vertebra. Whereas the anterior

vertebral centra are relatively small, the centra in the sacral region are about as large as the largest centra known from *Ophthalmosaurus icenicus*, despite the body being comparatively smaller. The caudal vertebral centra gradually decrease in height posteriorly. Neural spines are preserved with most of the vertebral centra, and are exposed laterally. Their bases are broad columns and broaden dorsally into square neural spines that are angled slightly posterodorsally. There appears to be little overlap between the neural spines dorsally.

Ribs. Many ribs are preserved in the holotype specimen and are generally the same widely curved form as found in *Ophthalmosaurus icenicus* (Text-fig. 43). The ribs reach their largest size in the middle of the presacral region, becoming slightly longer and broader. Proximally, they largely overlap each other and some of the vertebrae, due to taphonomic displacement, obscure the articular surfaces. The proximal portion of the rib has a median groove that runs distally for about one-half of the length of the rib; this part of the rib is slightly more strongly convex than more distally. In the distal part, the ribs become straighter with rounded cross sections. At the distal extremity, some ribs are slightly expanded.

Coracoid. The coracoids too are relatively smaller in *Nannopterygius enthekiodon* than in *Ophthalmosaurus icenicus* and other ichthyosaurs (Text-figs 43, 44). Both are preserved ventral to the skull in NHMUK PV 46497, articulated with each other along the midline. The coracoids are also relatively longer and narrower in *Nannopterygius enthekiodon* than in *Ophthalmosaurus icenicus*, largely because of a medial anterior extension. Based on Kirton (1983), the length to width ratios are: $130.0 \text{ mm} / 77.8 \text{ mm} = 1.67$ in *Nannopterygius enthekiodon* compared to $190.0 \text{ mm} / 180.0 \text{ mm} = 1.06$ in *Ophthalmosaurus icenicus* (NHMUK PV R4753). They are plate-like and subquadrangular bones that meet each other medially along their entire length, rather than the defined facet along part of the medial

margin as seen in *Ophthalmosaurus icenicus*. Anteriorly, the medial portion of the coracoid is drawn anteriorly into a broad and square anteromedial process, the anterior margin of which would contact the clavicle. Lateral to this is a deep embayment in the coracoid, equivalent to the anterior notch in *Ophthalmosaurus icenicus*, which separates the anteromedial process from the lateral facets. This embayment shows that the lateral facets project far laterally (Kirton 1983). These facets are placed at about the midpoint of the lateral margin and are directed laterally and slightly anteriorly. The facets are elongate anteroposteriorly, but the separation between the scapular and glenoid contributions cannot be determined. Posterior to the glenoid facet, a slight emargination is developed in which the bone is unfinished, unlike the anterior embayment. The posterior margin appears rather straight and oblique; however, it is uncertain whether this is its true posterior border as the plaster surrounding it lies flush against the specimen.

Scapula. The proximal portion of the left scapula is partly exposed in NHMUK PV 46497 (Text-fig. 44). This is expanded and fan-like proximally, but narrows distally into an elongate blade. The proximal portion is crushed, but shows an anterior ridge interpreted as the facet for the clavicle, which may be associated with a well-developed acromion process, similar to that seen in *Ophthalmosaurus icenicus*. Posterior to this, the scapula has a large, rounded concavity. The proximal margin is either crushed or is missing. Compared to *Ophthalmosaurus icenicus*, the scapula, and pectoral girdle generally, are much smaller relative to the rest of the body.

Humerus. The humerus is slightly smaller relative to body size than in other ichthyosaur taxa (Text-figs 43, 44). Kirton (1983) compared its size relative to the jaw length: $69.6 \text{ mm}/600 \text{ mm} = 0.116$ in *Nannopterygius enthekiodon* (NHMUK PV 46497) compared to

150 mm/940 mm = 0.159 in *Ophthalmosaurus icenicus* (NHMUK PV R4753). The humerus in *Nannopterygius enthekiodon* retains much the same form seen in the other taxa described here. Both humeri in the holotype are interpreted to only be visible in ventral view.

Proximally, the humerus is broad and slightly convex, but less than the femur (see below), and extended anteroventrally by the triangular deltopectoral crest. The proximal and distal ends are expanded. Distally, the humerus is expanded slightly, to about the same width as the proximal end, and has two distal facets, unlike the three facets in *Ophthalmosaurus icenicus* and *Brachypterygius extremus*. The posterior facet, which articulates with the ulna, is larger, and faces posterodistally. Anterior to this, the radial facet is separated by a low ridge and faces anterodistally creating a distinct apex between the two facets.

Forelimb epipodials and mesopodials. The epipodials in NHMUK PV 46497 are poorly preserved, and only the left forelimb preserves both *in situ* (Text-fig. 44). The radius is the anterior element and is slightly smaller than the ulna. Both elements are rounded, subquadrate, and slightly thickened. The right forelimb in the holotype is disarticulated, but preserves several more distal elements. These are all well-rounded and slightly thickened. Two proximal and one distal carpals are present in the left forelimb, arranged in columns parallel to the long axis of the humerus.

Pelvic girdle. A small fragment of bone in NHMUK PV R1197 may be part of the ischium, but is not complete enough to be described. The holotype has been repaired in this region so the elements are likely lost.

Femur. The femur is small and robust, similar in form to the other taxa described in this monograph (Text-fig. 43; Pl. 39, figs 1–5). Kirton (1983) also compared this to the jaw

length: $10 \times 47.9 \text{ mm} / 600 \text{ mm} = 0.798$ in *Nannopterygius enthekiodon* (NHMUK PV 46497) and $10 \times 84.2 \text{ mm} / 940 \text{ mm} = 0.896$ in *Ophthalmosaurus icenicus* (NHMUK PV R4752). The proximal surface is large, convex, and pitted where it was covered by the articular cartilage, becoming broader dorsoventrally by the large dorsal and ventral processes. The dorsal process is large and triangular, with much of the proximal portion contiguous with the pitted proximal surface. This process is placed along the approximate midline of the femur, as in *Ophthalmosaurus icenicus*, and is directed distally, approximately parallel to the long axis of the femur. The distal slope is also more sharply ridged in *Nannopterygius enthekiodon*, extending for half the femoral length. The ventral process is large and well developed towards the anteroventral margin of the femur creating a broad anterior face on the femur that is slightly concave to the midline. Distally, the diaphysis is slightly constricted, but not as strongly in the humerus, or in *Ophthalmosaurus icenicus*. The broad anterior face makes the anterior margin here well rounded, while the posterior edge is sharper. The femur expands distally to about the same width as the proximal head. There are two equal-sized distal facets that articulate with the tibia (anterior) and fibula, separated by a ridge. Each facet faces distally with the fibular facet directed slightly anteriorly and the tibial facet slightly posteriorly.

Hindlimb epipodials and mesopodials. The fibula and tibia articulate with the distal femur (Pl. 39, figs 1–5). Both are rounded discoidal elements, similar to *Ophthalmosaurus icenicus*. The tibia is the anteriormost, smaller, subpentagonal element and meets the femur, intermedium, and fibula. Posterior to this, the fibula is about twice the size of the tibia and subpentagonal. It contacts the femur, tibia, intermedium, and second distal carpal.

The astragalus, second distal tarsal, and another distal tarsal are preserved in NHMUK PV 46497a. They are rounded elements, much smaller than the tibia and placed distally.

Proximally, the astragalus is pointed and projects between the distal fibula and tibia. These elements have not been prepared sufficiently to allow further description.

Genus MACROPTERYGIUS Huene, 1922b

Macropterygius sp. indet.

Pl. 40

Material. Three humeri: NHMUK PV 42286, a left humerus from the Kimmeridge Clay Formation of the Isle of Portland, Dorset; OUMNH J12031, a left humerus from the Kimmeridge Clay Formation of Cumnor, Oxfordshire, and J68534, a right humerus from recent gravels at St Helens, Abingdon, Oxfordshire, but most likely derived from the Kimmeridge Clay Formation.

Diagnosis. Member of Ophthalmosauridae characterized by: humerus with large, well developed dorsal and ventral processes (small deltopectoral crest in *Cryopterygius*); two distal humeral facets (shared with *Cryopterygius*, *Nannopterygius*, *Platypterygius*); anterior distal humeral facet larger than posterior distal humeral facet (shared with *Cryopterygius*).

Etymology. The generic name *Macropterygius* is derived from the Greek μάκρος ‘long’ and πτέρυγα ‘wing’, from the large number of digit elements.

Occurrence. Kimmeridgian (Upper Jurassic) of Dorset and Oxfordshire, United Kingdom, and France.

Discussion. Owen (1840, p. 124) erected *Ichthyosaurus trigonus* on a cervical vertebra from the collection of Ms Eltheldred Benett (Spamer *et al.* 1989; Spamer & Torrens 1991; International Commission on Zoological Nomenclature 1993; Spamer *et al.* 1995). When this specimen was thought lost, Phillips (1871, p. 335) applied *Ichthyosaurus trigonus* to several vertebrae from the Kimmeridge Clay Formation; none of this material is diagnostic, therefore *Ichthyosaurus trigonus* is considered a *nomen dubium* (see *Taxa invalida* below). Much other material was subsequently referred to *Ichthyosaurus trigonus* (e.g. Lydekker 1889; Sauvage 1888, 1894, 1902a, b, c, d, 1911), including particularly humeral material. Huene (1922b, p. 98) erected the genus *Macropterygius* to include *Ichthyosaurus trigonus*, *Ichthyosaurus dilatatus*, and *Ichthyosaurus ovalis*, among other taxa, none of which are valid (see *Taxa invalida* below and McGowan 1976; McGowan & Motani 2003). However, Huene (1922b, p. 98) included a diagnosis for *Macropterygius*, based in part on the forelimb material of Sauvage (1911). This diagnosis agrees with the humeral material referred here to *Macropterygius* sp. indet. and described below (NHMUK PV 42286, and OUMNH J12031 and J68534), and is different enough to warrant a separate genus. Therefore, we retain *Macropterygius* as a valid genus, however, we do not consider the available material to be complete enough to identify or erect a new species. Until more complete material becomes available, we refer these specimens to *Macropterygius* sp. indet., and provide a basic diagnosis of the genus *Macropterygius*.

Huene (1922b, p. 98) characterized *Macropterygius* by a robust snout; smaller orbit than *Ophthalmosaurus* (found in almost all Ichthyosauria); maxilla does not contact the external naris (found in several ichthyosaur taxa, mostly within Parvipelvia, e.g. *Temnodontosaurus*, *Brachypterygius*, *Maiaspondylus*); teeth with cementum around the root dentine and sharp, narrow ridges on the crown (plications; primitive for Ichthyosauria, re-evolved in Platypterygiinae: Maxwell *et al.* 2011a, 2012a); bicipital ribs, except the posterior (found in

Parvipelvica); coracoid shorter and broader than in *Nannopterygius* (similar to other Ophthalmosauridae); shoulder girdle with three separate bones (status uncertain: this is assumed to refer to the clavicle, scapula, and coracoid on each side, in which case this is primitive to Ichthyosauriformes); humerus with strong and large lateral process (dorsal or ventral process?; shared with Ophthalmosauridae), articulates distally with two bones (similar to *Cryptopterygius*, *Platypterygius*); latipinnate and elongate forelimb construction. Delair (1959, p. 66) later assigned *Ichthyosaurus thyreospondylus* to *Macropterygius*. McGowan (1976, p. 670) considered all species assigned to this genus to be *taxa dubia* thereby making *Macropterygius* a *taxon dubium* also; Kirton (1983, p. 139) and McGowan & Motani (2003, p. 129) also considered *Macropterygius* a *nomen dubium*. The humeri described below are consistent with Huene's (1922b, p. 98) diagnosis for *Macropterygius*, based upon the material of Sauvage (1911).

One humerus in the NHMUK, PV 42286, and two humeri in the OUMNH collections, J12031 and J68534, can be clearly separated from other ichthyosaur taxa. The OUMNH specimens are each accompanied by a note: "Almost certainly *Platypterygius*. C. McGowan 31/8/2000". These humeri clearly have only two distal facets, unlike *Ophthalmosaurus icenicus* and *Brachypterygius extremus* (see above). Furthermore, the anterior facet, probably articulating with the radius, is much larger than the posterior facet (see description below). This precludes assigning these specimens to *Platypterygius*, in which the posterior (ulnar) facet is larger (McGowan & Motani 2003). This configuration of the distal humeral facets is also different from *Aegirosaurus leptospondylus*, in which there are clearly three distal humeral facets, as in *Brachypterygius extremus*, and the radial and ulnar facets are similarly sized, or the ulnar facet may be larger (Bardet & Fernández 2000). Taxa in which the radial facet is larger than the ulnar include *Ophthalmosaurus icenicus*, *Caypullisaurus bonapartei*, *Arthropterygius chrisorum*, and *Acamptonectes densus*. These four taxa all have three distal

facets that articulate with the anterior accessory element, radius, and ulna respectively (Russell 1993; Fernández 1997b; McGowan & Motani 2003; Maxwell 2010; Fischer *et al.* 2012). The size of the anterior facet is variable within and between species, and may be strongly reduced. None of these specimens show any evidence for a rudimentary facet anterior to the radial facet. The most similar form to this humerus is found in *Cryopterygius kristiansenae*, which has comparably sized distal facets, although the radial facet is not as large in this taxon as in NHMUK PV 42286, and OUMNH J12031 and J68534. However, in *Cryopterygius kristiansenae* the deltopectoral crest is much smaller than in those specimens, without the distinct anterior and posterior concavities, and is more posteriorly placed (Druckenmiller *et al.* 2012). Similarly, while *Nannopterygius enthekiodon* also possesses two distal humeral facets, the ulnar facet is the larger and the deltopectoral crest does not appear as large as in these *Macropterygius* sp. indet. specimens (see the description of the humerus of *Nannopterygius enthekiodon* above). The recently described *Sisteronia seeleyi* Fischer *et al.*, 2014a does have a larger radial facet than the ulnar facet, however, this taxon also possesses a posterior distal humeral facet, but the anterior and proximal regions are broken, which make uncertain the presence of an anterior facet. The morphology of these humeri does have clear affinities to the specimen described by Sauvage (1911, pp. 434–441) as *Ichthyosaurus trigonus* (see below); these were separated by Huene (1922, p. 98) as *Macropterygius*. Referral of *Macropterygius* to Ophthalmosauridae is based upon the large, plate-like dorsal process and large deltopectoral crest, surrounded by concavities (Fischer *et al.* 2013). The latter character may indicate affinities to the clade Platypterygiinae, whereas the lack of anterior accessory element suggests it is more basal within Ophthalmosauridae.

Description. Humerus. The humeri are short and robust, and expanded proximally and distally with a slightly constricted diaphysis (Pl. 40). The proximal surface is convex and

irregularly pitted for application of cartilage. Dorsally, this surface extends onto the high dorsal process, which is worn and broken in all specimens, and extends distally, and slightly anteriorly, for about one-half of the humeral length, as in *Ophthalmosaurus icenicus* and *Brachypterygius extremus*. There is also a high deltopectoral crest ventrally, placed anteriorly, and with a similar, plate-like form to the dorsal process, with large concavities anteriorly and posteriorly. Compared to *Ophthalmosaurus icenicus*, the proximal edges of these processes slope more distally, giving the proximal humerus a narrower and more rounded appearance in anterior and posterior view. The processes do not seem as large as in *Ophthalmosaurus icenicus* or *Brachypterygius extremus*, but this may be due to crushing and breakage. The diaphysis is the same as in *Ophthalmosaurus icenicus*, with a broad, rounded anterior edge, and sharper posterior edge. There is rather less expansion of the humerus distally than in *Ophthalmosaurus icenicus* and *Brachypterygius extremus*, so the constriction at the diaphysis appears less pronounced.

Distally, the humerus expands, more strongly anteriorly, and broadens to accommodate the distal facets. Both the anterodistal and posterodistal apices are acute, but less acute than in the above taxa. There are two large, concave distal facets, subtriangular in shape and rugose where cartilage would be present, separated by a distinct ridge. The anterior facet would probably articulate with the radius and faces distally and slightly anteriorly. This is much wider dorsoventrally than the posterior facet. The posterior facet, about two-thirds the size of the anterior, probably articulated with the ulna, and faces more strongly posterodistally, so that a clear obtuse angle is subtended in the distal margin in dorsoventral view. A much lower, incomplete ridge is present slightly posterior to the main ridge between these facets in OUMNH J68534. This may indicate articulation with a third element distally. Compared to the other facets, the area formed is tiny and directed slightly posteriorly, unlike the form

taken in *Brachypterygius extremus*. As the posterior ridge is incomplete, it suggests any contact would not be close, and may be a result of variation in the paddle configuration.

TAXA INVALIDA

The following are invalid names for British Middle and Upper Jurassic taxa, which are listed under each genus in alphabetical order of the species name. Discussion on global taxa is given by McGowan (1976) and McGowan & Motani (2003).

Genus ICHTHYOSAURUS König, 1818

Ichthyosaurus advena Phillips, 1871

- | | |
|------|---|
| 1871 | <i>Ichthyosaurus advena</i> Phillips; p. 183 [Stonesfield Member, Taynton Limestone Formation (Bathonian Stage), Stonesfield, Oxfordshire, UK]. |
| 1976 | <i>Ichthyosaurus advena</i> Phillips; McGowan, p. 670 [<i>nom. nud.</i>]. |
| 2003 | <i>Ichthyosaurus advena</i> Phillips; McGowan & Motani, p. 139 [<i>nom. nud.</i>]. |

Status. *Nomen nudum.*

Material. Vertebrae from the Stonesfield Member, Taynton Limestone Formation (Bathonian Stage) of Stonesfield, United Kingdom, designated by Phillips (1871, p. 183).

Discussion. Phillips (1871) proposed this taxon for ichthyosaur vertebrae from the Stonesfield Slate of Stonesfield, but did not provide a definition, description, or figure, nor

did he assign a type specimen. *Ichthyosaurus advena* should therefore be considered a *nomen nudum*; McGowan (1976, p. 670) also considered this a *nomen nudum*.

Ichthyosaurus aequalis Phillips, 1871

- * 1871 *Ichthyosaurus aequalis* Phillips; p. 339 [Kimmeridge Clay Formation (Kimmeridgian Stage), Shotover, Oxfordshire, UK].
- 1959 *Ichthyosaurus aequalis* Phillips; Delair,
- 1976 *Ichthyosaurus aequalis* Phillips; McGowan [*tax. dub.*].
- [1983 *Ichthyosaurus aequalis* Phillips; Kirton, p. 136 [*nom. dub.*].]
- 2003 *Ichthyosaurus aequalis* Phillips; McGowan & Motani, p. 130 [*nom. dub.*].

Status. Nomen dubium.

Material. One caudal vertebra designated by Phillips (1871, p. 339) from the Kimmeridge Clay Formation of Shotover, Oxfordshire, United Kingdom. Phillips did not designate a type; the only known specimen assigned to this taxon is OUMNH J12424.

Discussion. Phillips (1871) separated this species by a single excavated apophysis placed halfway on the side of the central body. This feature is seen generally in the middle caudal region of Jurassic ichthyosaur taxa, and should not be regarded as distinctive. McGowan (1976, p. 670) and Kirton (1983, p. 138) found this taxon to be a *taxon dubium* and *nomen dubium* respectively.

Ichthyosaurus chalarodeirus Seeley, 1869

- 1869 *Ichthyosaurus chalarodeirus* Seeley; p. 106 [Kimmeridge Clay Formation (Kimmeridgian Stage), Chettisham, Cambridgeshire, UK].
- 1888 *Ichthyosaurus calorodirus* [sic.] Seeley; Lydekker, p. 312 [*lapsus calami*].
- 1922b '*Ichthyosaurus*' *chalarodirus* [sic.] Seeley; Huene, p. 93.
- 1976 *Ichthyosaurus chalarodeirus* Seeley; McGowan [*nom. nud.*].
- [1983 *Ichthyosaurus chalarodeirus* Seeley; Kirton, p. 136 [*nom. nud.*].]
- 2003 *Ichthyosaurus chalarodeirus* Seeley; McGowan & Motani, p. 139 [*nom. nud.*].

Status. Nomen nudum.

Material. CAMSM J29777: an unfused axis vertebra designated by Seeley (1869, p. 106) from the Kimmeridge Clay Formation of Chettisham, Cambridgeshire, United Kingdom.

Discussion. Seeley (1869, p. 106) did not include a description, diagnosis, or figure for the naming of *Ichthyosaurus chalarodeirus* Seeley, 1869, so this action does not constitute an indication under Article 12.3 of the International Code of Zoological Nomenclature (ICZN) (International Commission on Zoological Nomenclature 1999, amended 2012). Therefore, *Ichthyosaurus chalarodeirus* should be considered a *nomen nudum*; this was also concluded by McGowan (1976, p. 670). The same applies also to *Ichthyosaurus hygrodeirus* Seeley, 1869 (see below).

***Ichthyosaurus dilatatus* Phillips, 1871**

- * 1871 *Ichthyosaurus dilatatus* Phillips; pp. 307 [Oxford Clay Formation (Callovian Stage), Oxford, UK], 339 [Kimmeridge Clay Formation (Kimmeridgian Stage), Shotover, Oxfordshire, UK].
- 1889 *Ichthyosaurus?* *dilatatus* Phillips; Lydekker, p. 30.

- 1894 *Ophthalmosaurus dilatatus* (Phillips); Sauvage, p. 926 [Middle Portlandian, Boulonnais, France].
- 1898 *Ichthyosaurus trigonus* Owen; Bauer, p. 325 [senior subjective synonym].
- 1959 *Macropterygius dilatatus* (Phillips); Delair, p. 65.
- 1976 *Ichthyosaurus dilatatus* Phillips; McGowan [*tax. dub.*].
- [1983 *Ichthyosaurus dilatatus* Phillips; Kirton, p. 137 [*nom. dub.*].]
- 2003 *Ichthyosaurus dilatatus* Phillips; McGowan & Motani, p. 131 [*nom. dub.*].

Status. Nomen dubium.

Material. “A considerable number” of dorsal and caudal vertebrae were assigned to this species by Phillips (1871, p. 339) from the Kimmeridge Clay Formation of Oxfordshire, United Kingdom. Also, three cervical and ten dorsal vertebrae from the Oxford Clay Formation at St Clements, Oxford, United Kingdom (Phillips 1871, p. 307). Delair (1959) cited OUMNH J12494 as the type specimen. Specimens have been found in Cowley Fields, Oxford (OUMNH J12494) and Swindon (NHMUK PV 45984–7), United Kingdom.

Discussion. This taxon is separated by having broader vertebrae than *Ichthyosaurus trigonus* and thicker vertebrae than *Ichthyosaurus thyreospondylus*. Phillips (1871, p. 307) also listed dimensions for the cervical vertebrae; no figures are given. These specimens are non-diagnostic and insufficient to separate the taxon (McGowan 1976, p. 670; Kirton 1983, p. 137) and so *Ichthyosaurus dilatatus* Phillips, 1871 should be considered a *nomen dubium*. Specimen NHMUK PV 45984–7, assigned to *Ichthyosaurus? dilatatus*, may be referred to *Brachypterygius extremus*.

Ichthyosaurus hygrodeirus Seeley, 1869

- 1869 *Ichthyosaurus hygrodeirus* Seeley; p. 106 [Kimmeridge Clay Formation (Kimmeridgian Stage), Stretham, Cambridgeshire, UK].
- 1888 *Ichthyosaurus hygrodirus* [sic.] Seeley; Lydekker, p. 312 [*lapsus calami*].
- 1922b '*Ichthyosaurus*' *hyrodirus* [sic.] Seeley; Huene, p. 94.
- 1976 *Ichthyosaurus hygrodeirus* Seeley; McGowan [*nom. nud.*].
- [1983 *Ichthyosaurus hygrodeirus* Seeley; Kirton, p. 137 [*nom. nud.*].]
- 2003 *Ichthyosaurus hygrodeirus* Seeley, McGowan & Motani, p. 139 [*nom. nud.*].

Status. Nomen nudum.

Material. Specimen CAMSM J29780: an unfused axis vertebra designated by Seeley (1869, p. 106) from the Kimmeridge Clay Formation of Stretham, Cambridgeshire, United Kingdom.

Discussion. See the discussion above for *Ichthyosaurus chalarodeirus*.

Ichthyosaurus megalodeirus Seeley, 1869 **Pls 26–28** in Part 1

- 1869 *Ichthyosaurus megalodeirus* Seeley; p. 111 [Oxford Clay Formation (Callovian Stage), Peterborough, Cambridgeshire, UK].
- 1888 *Ichthyosaurus megalodirus* [sic.] Seeley; Lydekker, p. 312 [*lapsus calami*].
- 1922b '*Ichthyosaurus*' *megalodirus* [sic.] Seeley [sic.]; Huene, p. 93 ["probably an *Ophthalmosaurus*"].
- [1983 *Ophthalmosaurus icenicus* Seeley; Kirton, p. 137 [*Ichthyosaurus megalodeirus* is a senior synonym, but rejected under ICZN Article 23(a–b) (= Article 23.9; International Commission on Zoological Nomenclature 1999, amended 2012)].]
- 2003 *Ophthalmosaurus icenicus* Seeley; McGowan & Motani, p. 113 [*nom. nud.*].

Status. Nomen nudum.

Material. Specimens CAMSM J65710–J65765: one individual including skull elements (Pls 26, 27 in Part 1), 95 vertebrae (including the atlas-axis complex), and various girdle elements (Pl. 28 in Part 1; listed in Seeley 1869, pp. 111–115) from the Oxford Clay Formation of Peterborough, United Kingdom. Designated by Seeley (1869, p. 111) as *Ichthyosaurus megalodeirus* Seeley, 1869.

Discussion. Seeley (1869) did not describe or figure this specimen beyond listing what elements were present, which does not meet the requirements for an indication under Article 12.3 of the ICZN (International Commission on Zoological Nomenclature 1999, amended 2012). This taxon should thus be considered a *nomen nudum* (McGowan & Motani 2003, p. 113), not a senior synonym for *Ophthalmosaurus icenicus* as proposed by Kirton (1983, p. 137). In this case, ICZN Article 23.9 ('Reversal of precedence'; International Commission on Zoological Nomenclature 1999, amended 2012) need not be enacted. Examination of the material for this taxon shows it is consistent with the type and referred material of *Ophthalmosaurus icenicus* and the material may be referred to that taxon. See also the taxonomic discussion of *Ophthalmosaurus icenicus* in Part 1.

Ichthyosaurus ovalis Phillips, 1871

- * 1871 *Ichthyosaurus ovalis* Phillips; p. 339 [Kimmeridge Clay Formation (Kimmeridgian Stage), Swindon, Wiltshire, Shotover, Oxfordshire, and Kimmeridge, Dorset, UK].
- 1889 *Ichthyosaurus ovalis* Phillips; Lydekker, p. 29, fig. 15.
- 1898 *Ichthyosaurus trigonus* Owen; Bauer, p. 325 [senior subjective synonym].

- 1922b *Macropterygius? ovalis* (Phillips); Huene, p. 98.
- 1959 *Macropterygius ovalis* (Phillips); Delair, p. 65.
- [1983 *Ichthyosaurus ovalis* Phillips; Kirton, p. 138 [*nom. dub.*].]
- 2003 *Ichthyosaurus ovalis* Phillips; McGowan & Motani, p. 133 [*nom. dub.*].

Status. Nomen dubium.

Material. Vertebrae from the Kimmeridge Clay Formation of Swindon, Shotover and Kimmeridge, United Kingdom, designated by Phillips (1871, p. 339), probably OUMNH J12487, J12488/1–2, and J12489/1–2 (assigned by Delair 1959). Also, NHMUK PV 42282, a dorsal vertebra, and 44637, 43 anterior dorsal to caudal vertebral centra; OUMNH J10473, J10480, J10482/1–2, and J12421, all vertebrae, are referred to this taxon.

Discussion. Phillips (1871) did not designate a type specimen or figure the vertebrae he assigned to this taxon, although he did give measurements for one centrum (OUMNH J12488/1). *Ichthyosaurus ovalis* is separated by the oval outline of the vertebrae, higher than broad, and two posterior dorsal vertebrae have ventrally placed rib facets “in the situation occupied by the hæmapophysis of a crocodilian reptile” (Phillips 1871, p. 339). These specimens are not distinctive, nor diagnostic, therefore *Ichthyosaurus ovalis* should be regarded as a *nomen dubium*. McGowan (1976) regarded this as a *taxon dubium*.

***Ichthyosaurus thyreospondylus* Owen, 1840**

- * 1840 *Ichthyosaurus thyreospondylus* Owen; p. 124 [unknown horizon and locality].
- 1871 *Ichthyosaurus thyreospondylus* Owen; Phillips, pp. 307 [Oxford Clay Formation (Callovian Stage), Buckingham, UK], 337, figs 129–131 [Kimmeridge Clay Formation (Kimmeridgian Stage), Oxfordshire and Weymouth, Dorset, UK].

- ? 1881 *Ichthyosaurus brachyspondylus* Owen; p. 127, pl. 33, figs 3–6 [Liassic formations (Lower Jurassic Series), UK, Russia].
- 1888 *Ichthyosaurus* aff. *thyreospondylus* Owen; Sauvage, p. 629 [Kimmeridgian, Wilmille, Auvringhen, France].
- 1889 *Ichthyosaurus thyreospondylus* Phillips (*ex* Owen); Lydekker, p. 34.
- 1902b *Ichthyosaurus thyreospondylus* [sic.] Owen; Sauvage, p. 403 [*lapsus calami*].
- 1911 *Ichthyosaurus thyreospondylus* Phillips [sic.]; Sauvage, p. 443 [Middle Portlandian, Boulogne, France] [authority listed as Phillips 1871].
- 1911 *Ophthalmosaurus thyreospondylus* [sic.] Owen; Sauvage p. 445 [*lapsus calami*].
- 1922b *Ophthalmosaurus thyreospondylus* (Owen); Huene, p. 91.
- 1959 *Macropterygius?* *thyreospondylus* (Owen); Delair, p. 66.
- 1976 *Ichthyosaurus thyreospondylus* Owen; McGowan, p. 670 [*tax. dub.*].
- [1983 *Ichthyosaurus thyreospondylus* Owen; Kirton, p. 138 [*nom. dub.*].
- 2003 *Ichthyosaurus thyreospondylus* Owen; McGowan & Motani, p. 134 [*nom. dub.*].

Status. Nomen dubium.

Material. Five vertebrae designated by Owen (1840, p. 124) in BRSMG that have since been destroyed (Kirton 1983). Several vertebrae figured by Phillips (1871, figs 129–131) are possibly Owen's holotype specimens (Woodward & Sherborn 1890; McGowan 1976). The following specimens have been assigned to this taxon: NHMUK PV R1684, a caudal vertebral centrum from the Portlandian of the Isle of Portland; OUMNH J10479, J10492, J10508, J12066, J12306, J12307, J12423, J12426, J12464, J12467, J12469, J12472, J12474, J12478, J12485, J12492, J12495 from the Kimmeridge Clay Formation, and J12496 from the Oxford Clay Formation, all of which are vertebrae.

Discussion. *Ichthyosaurus thyreospondylus* was separated by a dorsal triangular convexity on the anterior and posterior faces of the centra; this is found in all Upper Jurassic

taxa. None of the material listed above includes diagnostic remains, so *Ichthyosaurus thyreospondylus* is rejected as a *nomen dubium*. McGowan (1976) considered this a *taxon dubium*, Kirton (1983) a *nomen dubium*.

Ichthyosaurus trigonus Owen, 1840

- * 1840 *Ichthyosaurus trigonus* Owen; p. 124 [Kimmeridge Clay Formation (Kimmeridgian Stage), Westbrooke, in Bromham, Bedfordshire, UK].
- 1852 *Ichthyosaurus posthumus* Wagner; p. 702, pl. 4, figs 4, 5 [Solnhofen Limestone Formation (Tithonian Stage), Bavaria, Germany].
- non 1861a *Ichthyosaurus cuvieri* Valenciennes; p. 273 [Kimmeridge Clay Formation (Kimmeridgian Stage), Boulogne, France].
- non 1861b *Ichthyosaurus normanniae* Valenciennes; p. 1001 [Kimmeridge Clay Formation (Kimmeridgian Stage), Bléville, France].
- 1871 *Ichthyosaurus trigonus* Owen; Phillips, p. 335, figs 126–128 [Kimmeridge Clay Formation (Kimmeridgian Stage), Shotover, Oxfordshire and Swindon, Wiltshire, UK].
- 1889 *Ichthyosaurus trigonus* Owen; Lydekker, p. 22.
- ? 1889 *Ichthyosaurus cuvieri* Valenciennes; Lydekker, p. 22.
- ? 1889 *Ichthyosaurus normanniae* Valenciennes; Lydekker, p. 22.
- 1894 *Ichthyosaurus trigonus* Owen; Sauvage, p. 926.
- ? 1894 *Ichthyosaurus* aff. *trigonus* Owen; Sauvage, p. 926.
- 1898 *Ichthyosaurus trigonus* Owen; Bauer, p. 325.
- 1902b *Ichthyosaurus trigonus* Owen; Sauvage, p. 402 [Middle Kimmeridgian, Boulonnais].
- non 1902a *Ophthalmosaurus cuvieri* (Valenciennes); Sauvage, p. 29, pl. 5, fig. 7.
- non 1902c *Ophthalmosaurus cuvieri* (Valenciennes); Sauvage, p. 386.
- 1908 *Ichthyosaurus trigonus posthumus* (Owen); Merriam, p. 40.
- non 1911 *Ophthalmosaurus cuvieri* (Valenciennes); Sauvage, p. 426 [Middle Kimmeridgian, Le Havre, France].

- 1911 *Ichthyosaurus trigonus* Owen; Sauvage, p. 434 [Upper Kimmeridgian, Boulogne-sur-Mer, France].
- non 1911 *Ichthyosaurus normanniae* Valenciennes; Sauvage, p. 441 [Kimmeridge Clay Formation, Bléville, France].
- 1922b *Macropterygius trigonus* (Owen); Huene, p. 92–93.
- 1959 *Macropterygius trigonus* (Owen); Delair, p. 64.
- 1976 *Ichthyosaurus trigonus* Owen; McGowan, p. 670 [*tax. dub.*].
- [1983 *Ichthyosaurus trigonus* Owen; Kirton, p. 139 [*nom. dub.*].]
- 1989 *Ichthyosaurus trigonus* Owen; Spamer *et al.*, pp. 118, 144, 158, pl. 13, fig. 1a–c.
- 1991 *Macropterygius trigonus* (Owen); Spamer & Torrens.
- 2003 *Ichthyosaurus trigonus* Owen; McGowan & Motani, p. 134 [*nom. dub.*].

Status. Nomen dubium.

Material. A vertebral centrum from the Kimmeridge Clay Formation of Westbrooke, in Bromham, Bedfordshire, United Kingdom, in the collection of Ms Etheldred Benett, designated by Owen (1840, p. 124). The holotype was thought to be lost (Delair 1959, p. 64), so Lydekker (1889) proposed Phillips' (1871, p. 335) specimens as replacement: OUMNH J12064, J12483, J12491, a dorsal vertebra, ankylosed atlas-axis complex, and caudal vertebra respectively. Ms Benett's collection had been donated to the Academy of Natural Sciences of Philadelphia after her death. The holotype specimen of *Ichthyosaurus trigonus*, a single anterior vertebral centrum, was rediscovered following cataloguing of this collection, and the original holotype (ANSP 10124) reinstated (Spamer *et al.* 1989; Spamer & Torrens 1991; International Commission on Zoological Nomenclature 1993; Spamer *et al.* 1995). Numerous further specimens from the United Kingdom and France have been assigned to *Ichthyosaurus trigonus* and are present in NHMUK and OUMNH, mostly vertebrae, but see the discussion below.

Discussion. Owen (1840) separated this taxon based on the straight ventral margins on the centrum, converging at 70°, and the broad dorsal side. This is common to all ophthalmosaurid anterior vertebral centra; those immediately posterior to the atlas-axis. Phillips (1871, figs 126–128) did not figure the holotype (*contra* Woodward & Sherborn 1890; McGowan 1976). The holotype was figured by Spamer *et al.* (1989, pl. 13, fig. 1a–c). This vertebral material is non-diagnostic, leading McGowan (1976, p. 670) and Kirton (1983, p. 139) to consider this a *taxon dubium* and *nomen dubium* respectively. Bauer (1898) considered several Upper Jurassic species to be referable to this species, including *Ichthyosaurus cuvieri*, *Ichthyosaurus dilatatus*, *Ichthyosaurus normanniae*, *Ichthyosaurus ovalis*, *Ichthyosaurus posthumus*, *Ichthyosaurus thyreospondylus*, and all species in *Ophthalmosaurus*. Many specimens have been assigned to this taxon, among which is NHMUK PV 42284, a humerus that has here been referred to *Macropterygius* sp. indet. (see above).

Following Valenciennes' (1861a, b) description of *Ichthyosaurus cuvieri* and *Ichthyosaurus normanniae* (figured in Lennier 1870, pl. 6), Sauvage (1874, p. 84, footnote 1) suggested that these taxa may be synonymous with *Ichthyosaurus trigonus* and *Ichthyosaurus thyreospondylus* respectively. Lydekker (1889, pp. 22–23) agreed with this, but put forward that the specimen of *Ichthyosaurus normanniae* described by Valenciennes (1861b) was the same individual as *Ichthyosaurus cuvieri* described earlier (Valenciennes 1861a). Lydekker (1889) therefore tentatively included all three species under *Ichthyosaurus trigonus*. Subsequently, Sauvage (1888, 1894, 1902a, b, c, d) was toing and froing with the synonymy of *Ichthyosaurus cuvieri* and *Ichthyosaurus trigonus*, but finally retained them as distinct species (Sauvage 1911). Meanwhile, he referred *Ichthyosaurus cuvieri* to *Ophthalmosaurus cuvieri* (Valenciennes, 1861a) (Sauvage 1894). The type specimens of *Ichthyosaurus cuvieri*

and *Ichthyosaurus normanniae* were destroyed in World War II, but casts of the material remain in the Musée National d'Histoire Naturelle, Paris (Bardet *et al.* 1997; McGowan & Motani 2003).

Most of the specimens referred to *Ichthyosaurus trigonus* are vertebrae that show no differing characteristics from other Middle to Late Jurassic ichthyosaurs. The characters detailed by previous authors are largely attributable to individual variation or related to the position in the vertebral column (Lydekker 1889; Sauvage 1911; Delair 1959). More substantial material, such as the partial forelimb described by Sauvage (1911) indicates the presence of another taxon of ichthyosaur in the Upper Jurassic of the United Kingdom and France, besides *Brachypterygius* and *Nannopterygius*. The morphological affinity between this and several other specimens referred to *Ichthyosaurus trigonus* may allow erection of a new species of ichthyosaur. In this monograph, we have separated this material as *Macropterygius* sp. indet. (see above).

Genus OPHTHALMOSAURUS Seeley, 1874b

Ophthalmosaurus monocharactus Appleby, 1956 Pls 29, 30 in Part 1

- * 1956 *Ophthalmosaurus monocharactus* Appleby; p. 444 [Oxford Clay Formation (Callovian Stage), Peterborough, Cambridgeshire, UK].
- 1958 *Ophthalmosaurus monocharactus* Appleby; pp. 9–10, 35.
- 1982 *Ophthalmosaurus* [sic.] *monocharactus* Appleby; Mazin, p. 97 [authority given as Appleby, 1965 (sic.)].
- [1983 *Ophthalmosaurus icenicus* Seeley; Kirton, pp. 11, 138 [senior subjective synonym].]
- non 1988 *Ophthalmosaurus monocharactus* Appleby; Gasparini, p. 3 [Vaca Muerta Formation, Cantera El Ministerio, Argentina (38° 49' S, 70° 12' E)].
- 1991 *Ophthalmosaurus monocharactus* Appleby; Martill, p. 229.

2003 *Ophthalmosaurus icenicus* Seeley; McGowan & Motani, p. 113 [senior subjective synonym].

Status. Junior subjective synonym of *Ophthalmosaurus icenicus*.

Material. Appleby (1956, p. 444) assigned PETMG R220 (formerly part of P.8; Appleby 1956, 1958) as the holotype specimen (Pls 29, 30 in Part 1).

Discussion. See the taxonomic discussion of *Ophthalmosaurus icenicus* in Part 1.

***Ophthalmosaurus pleydelli* Lydekker, 1890**

- * 1890 *Ophthalmosaurus pleydelli* Lydekker; p. 268, fig. 63 [Kimmeridge Clay Formation (Kimmeridgian Stage), Gillingham, Dorset, UK].
- 1890 *Ophthalmosaurus pleydelli* Lydekker; Mansell-Pleydell, p. 14, figs 3, 4.
- 1959 *Ophthalmosaurus pleydelli* Lydekker; Delair, p. 67.
- [1983 *Ophthalmosaurus icenicus* Seeley; Kirton, p. 14 [senior subjective synonym].]
- 2003 *Ophthalmosaurus icenicus* Seeley; McGowan & Motani, p. 113 [senior subjective synonym].

Status. Junior subjective synonym of *Ophthalmosaurus icenicus*.

Material. Lydekker (1890, p. 269) allocated a humerus (DORCM G.82) and anterior presacral vertebral centrum from the Kimmeridge Clay Formation of Gillingham, Dorset, United Kingdom; NHMUK PV R1712 and R1712a are casts of these. Lydekker (1890, p. 269) also suggested that NHMUK PV 46491, 46473, 46407, 47885, and 46474 may be referable to this species. The holotype was described by Mansell-Pleydell (1890).

Discussion. See the taxonomic discussion of *Ophthalmosaurus icenicus* in Part 1.

OSTEOLOGICAL COMPARISONS

The valid taxa described in Parts 1 and 2 – *Brachypterygius extremus*, *Ophthalmosaurus icenicus*, *Nannopterygius enthekiodon*, and *Macropterygius* sp. indet. – are compared to other relevant ichthyosaur taxa below. Most extensive comparisons are made with members of Ophthalmosauridae, with which the above taxa share the greatest affinity, and other relevant and well-known ichthyosaur taxa, particularly *Ichthyosaurus communis*. Further, more brief comparisons are made with more basal taxa as exemplars of various ichthyosaur ‘grades’ (after Motani 2005c): e.g. the basal grade *Grippia longirostris*, and intermediate grade *Cymbospondylus*, *Mixosaurus*, and *Shastasaurus*. Comparisons are made to highlight morphological differences between taxa, as are detailed between the taxa described above, but with a focus on characters used in recent phylogenetic analyses.

TRIASSIC ICHTHYOSAURS

Basal Ichthyosauriformes. The earliest and phylogenetically most basal Ichthyosauriformes together form a basal grade of ichthyosaur (*sensu* Motani 2005c) that together share many characteristics that differ from more derived taxa. This grade typically includes the Early Triassic taxa *Cartorhynchus lenticarpus* Motani *et al.*, 2015a, three species of *Chaohusaurus* Young & Dong, 1972 (Motani & You 1998b; Motani *et al.* 2015b), *Grippia longirostris* Wiman, 1929, *Gulosaurus helmi* Cuthbertson *et al.*, 2013b, *Parvinatator wapitiensis* Nicholls & Brinkman, 1995, and *Utatusaurus hataii* Shikama *et al.*, 1978. As

these taxa are neither phylogenetically nor temporally close to the taxa described above, only brief comparisons of the most important differences are made.

Unlike in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, the external naris in the earliest Ichthyosauriformes has a greater dorsal exposure, as in *Utatsusaurus hataii* and *Grippia longirostris* (Shikama *et al.* 1978; Motani *et al.* 1998; Motani 2000). The prefrontal and frontal both have greater dorsal exposure in more basal ichthyosaurs than in the *Brachypterygius extremus* or *Ophthalmosaurus icenicus* (Motani *et al.* 1998; Motani 2000; Maisch 2001). The frontal in these most basal taxa contributes to the margin of the orbit laterally, separating the prefrontal and postfrontal, but is excluded from the supratemporal fenestra, similar to *Ophthalmosaurus icenicus* (Text-fig. 4b; Wiman 1929; Mazin 1981; Motani *et al.* 1998; Motani 2000). In *Grippia longirostris*, *Parvinatator wapitiensis*, and *Utatsusaurus hataii*, the bones bordering the supratemporal fenestra are (left fenestra, clockwise from anterior): parietal, supratemporal, squamosal (in *Utatsusaurus hataii*, and likely in *Thalattoarchon saurophagis* [see below]), postorbital and postfrontal (Motani *et al.* 1998; Motani 2000; although see Cuthbertson *et al.* 2013a). *Utatsusaurus hataii* shows some fusion of the sutures in the skull, particularly between the dentary and surangular; this is greater in adult specimens than juveniles and therefore may be ontogenetic (McGowan & Motani 2003; Cuthbertson *et al.* 2013a). While all neoichthyosaurians, and most Upper Triassic ichthyosaurs, have the characteristic aulacodont tooth attachment (Edmund 1960), *Utatsusaurus hataii* and *Grippia longirostris* have subthecodont dentitions (Mazin 1983; Motani 1997, 1997b). The more basal ichthyopterygians have a broad and fan-like scapula dorsally with the glenoid articulation offset, rather than the narrower shaft of *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. This is best seen in *Grippia longirostris* and Mixosauridae *Mixosaurus cornalianus* and *Phalarodon atavus* (Reposi 1902; Wiman 1912, 1929; Mazin 1981; Nicholls *et al.* 1999; Liu *et al.* 2013). In basal Ichthyosauriformes and

Mixosauridae, the anterior margin of the humerus is drawn out anteriorly into a large flange, which hides the contours of the humeral shaft (Motani 1997a, 1998; Motani & You 1998a; McGowan & Motani 2003). The distal manual and pedal elements of basal grade ichthyosaurs are elongate and retain evidence of a demarcated shaft, although these elements are shorter compared to inferred terrestrial ancestors, such as *Petrolacosaurus* Reisz, 1977 (Shikama *et al.* 1978; Reisz 1981; Mazin 1986; Motani & You 1998a; Motani 1998, 1999a; Motani *et al.* 2014; Motani *et al.* 2015b). Basal ichthyosaurs have a distinct sacral region, and a larger and better-developed pelvic girdle than in *Ophthalmosaurus icenicus*, without fusion between the ischium and pubis (Wiman 1933; Shikama *et al.* 1978; Mazin 1981; Chen 1985; Motani *et al.* 1998).

Basal intermediate grade ichthyosaurs. Motani's (2005c) ichthyosaur grades include an intermediate grade that includes most Middle and Late Triassic ichthyosaur taxa. The intermediate ichthyosaur grade can be further separated into a Middle–Late Triassic merriamosaurian component (see *Basal Merriamosauria* below), and a solely Middle Triassic, non-merriamosaurian component. This includes Mixosauridae, *Cymbospondylus* Leidy, 1868, and *Thalattoarchon saurophagis* Fröbisch *et al.*, 2013, among others. Mixosauridae are distinct enough to be considered separately (see below), and Merriamosauria is considered below, so this discussion will include only non-merriamosaurian, non-mixosaurid ichthyosaurians.

Cymbospondylus petrinus Leidy, 1868 is notable for possessing additional ossifications posterior to the parietals, unlike in almost all other ichthyosaurs. The interpretations of Maisch & Matzke (2004) and Fröbisch *et al.* (2006) differ on whether this represents a single or paired postparietals respectively, or neomorphic bones. However, Fröbisch *et al.* (2006, p. 534) suggested there may be similar elements present in *Cymbospondylus buchseri* Sander,

1989 and *Cymbospondylus nichollsi* Fröbisch *et al.*, 2006. Maisch & Matzke (2006) identified similar elements in *Phantomosaurus neubigi* (Sander, 1997). *Thalattoarchon saurophagis* shows a slightly different configuration of the supratemporal fenestra to more basal and derived Ichthyosauriformes (Fröbisch *et al.* 2013): the squamosal is likely included in the border of the supratemporal fenestra (as in *Utatsusaurus hataii*; Motani *et al.* 1998; Cuthbertson *et al.* 2013a), and the frontal is developed posteriorly and separates the postfrontal and parietal at the anterior of the fenestra; in most other ichthyosaurs; the squamosal is excluded from the border of the supratemporal fenestra. The posterior portions of the vomers are visible in the holotype of *Cymbospondylus nichollsi* (Fröbisch *et al.* 2006). These are described as “wing-like” (Fröbisch *et al.* 2006, p. 524) and seem to show a wider posterior process than in *Ophthalmosaurus icenicus*; the suture between this and the palate is notched laterally. *Cymbospondylus petrinus* has a distinct posteromedial extension on each pterygoid that extends farther posteroventrally to the basisphenoid than seen in *Ophthalmosaurus icenicus* (Merriam 1908). *Thalattoarchon saurophagis*, *Himalayasaurus tibetensis* Young & Dong, 1972, and some examples of *Temnodontosaurus platyodon* and *Temnodontosaurus trigonodon* have laterally (labiolingually) compressed teeth (Theodori 1843; McGowan 1994b; Motani & Manabe 1999; McGowan & Motani 2003; Fröbisch *et al.* 2013) placing them in Massare’s (1987) ‘cut’ guild. The articular condyle of *Cymbospondylus petrinus* is very different to *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, as it is concave to receive the convex anterior face of the atlas for the articulation between the skull and vertebral column (Merriam 1908; Maisch & Matzke 2004). Maisch & Matzke (2004, p. 381) found the stapes of *Cymbospondylus petrinus* to be a long, thin and dorsally curved element that extends to a point high up on the quadrate. One of the most distinct characteristics of the neural arches is the pairing of the zygapophyses, particularly in the anterior presacral region, whereas the zygapophyses are separate in

Mixosaurus cornalianus and *Cymbospondylus petrinus*, but are joined medially in all adequately known neoichthyosaurians (Theodori 1843; Fraas 1891; Merriam 1902; Huene 1922b).

Mixosauridae. Mixosauridae (= Mixosauria *sensu* Motani 1999b) are a clade within Eoichthyosauria, included in Motani's (2005c) intermediate grade. This clade of typically small ichthyosaurs from the Middle Triassic is well defined and supported, with two genera included: *Mixosaurus* Baur, 1887a and *Phalarodon* Merriam, 1910, although the taxonomy of these is variable (McGowan & Motani 2003; Jiang *et al.* 2005; Jiang *et al.* 2006; Maisch 2010).

Unlike *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, *Phalarodon atavus* (Quenstedt, 1852) does not have either a supra- nor subnarial process posteriorly on the premaxilla. In the taxon, the premaxilla instead terminates posteriorly at the anterior margin of the external naris (Merriam 1908; Liu *et al.* 2013). In mixosaurids, the alveolar groove becomes much shallower than in *Brachypterygius extremus* or *Ophthalmosaurus icenicus*, and the teeth are set in shallow sockets and ankylosed to the bone (Fraas 1891; Repossi 1902; Motani 1997). The sockets in the anterior premaxilla and dentary in *Ophthalmosaurus icenicus* are a convergent feature. The frontals in Mixosauridae are strongly modified by the high sagittal and lateral ridges dorsally that delimit the well-developed anterior terrace of the supratemporal fenestra (Motani 1999c; Liu *et al.* 2013; see also Motani 1999b, fig. 3). In *Mixosaurus cornalianus* (Bassani, 1886) and *Phalarodon atavus* (Huene 1925; Motani 1999c; Maisch & Matzke 2001), the postfrontal is rather small, corresponding to the small size of the temporal fenestra and the short postorbital region. Isolated instances in *Phalarodon atavus* and *Mixosaurus cornalianus* show the squamosal to be a much narrower element than in other Hueneosauria, but still square, at the posterior of the skull (Huene

1949a; Motani 1999c; Liu *et al.* 2013). In *Mixosaurus panxianensis* Jiang *et al.*, 2006, the squamosal is lengthened ventrally to contact the embayment ventral to the cheek region alongside the postorbital (Jiang *et al.* 2006). The supratemporal fenestrae in these ichthyosaurs are positioned relatively far posteriorly, so that the postfrontal borders very little of it (Motani 1999c), but is raised to form the lateral margin of the anterior terrace of the supratemporal fenestra. The supratemporal fenestra in the mixosaurids *Mixosaurus cornalianus* and *Phalarodon atavus* is much smaller than most other ichthyosaurs, and corresponds to a small supratemporal, which nonetheless has considerable posterior exposure (Motani 1999c; Maisch & Matzke 2001; Liu *et al.* 2013). In dorsal view, the supratemporal fenestra in mixosaurids obscured by an anterodorsal sheet extension of the posterodorsal supratemporal that is not present in *Ophthalmosaurus icenicus* or *Brachypterygius extremus* (Motani 1999c; Maisch & Matzke 2001).

The palatines in *Mixosaurus cornalianus* have a much greater contribution, at their posterior margins, to the subtemporal fenestrae, compared to their almost complete exclusion by the pterygoids in *Ophthalmosaurus icenicus* (Maisch & Matzke 1997). Mixosauridae lack an interpterygoid vacuity, exemplified by *Phalarodon atavus* and *Mixosaurus cornalianus* (Maisch & Matzke 1997, 2001; Motani 1999b, character 27); the pterygoids meet each other medially for almost their entire lengths. In the otic capsule, there is a much closer contact between the opisthotic and the prootic bones in *Mixosaurus cornalianus* and *Phantomosaurus neubigi* (Maisch *et al.* 2006; Maisch & Matzke 2006) than in the ophthalmosaurid ichthyosaurs described above. A well-preserved specimen of *Mixosaurus cornalianus* (PIMUZ T4848; Maisch *et al.* 2006) also shows a greater expansion of the prootic anteriorly than in *Ophthalmosaurus icenicus*. Mixosaurids have a subthecodont tooth implantation (Motani 1997), variably developed. In particular, *Mixosaurus cornalianus* is characterized by a distinct narrowing of the alveolar groove between the teeth (Repossi 1902; Maisch &

Matzke 1997; Motani 1997). Jiang *et al.* (2005) and Maisch *et al.* (2008a) commented on the lack of clear sutures in the symphysial region of the dentary in '*Mixosaurus maotaiensis*' Young, 1965 and *Qianichthyosaurus zhoui*. Some ichthyosaurs have lower, rounded posterior teeth, for example, *Mixosaurus kuhnschneyuderi* (Brinkmann, 1998), *Phalarodon fraasi* Merriam, 1910, and *Xinminosaurus catactes* Jiang *et al.*, 2008 (Motani 2005b; Maisch & Matzke 2005) placing them in Massare's (1987) 'crush' guild; the anterior teeth in these taxa are conical.

Unlike most other ichthyosaur taxa, Mixosauridae have a medially narrow clavicle that may have had a broad ventral blade not present in *Brachypterygius extremus* or *Ophthalmosaurus icenicus* (Reposi 1902; Maisch *et al.* 2003). Despite the narrower median architecture of the clavicles than *Ophthalmosaurus icenicus*, mixosaurid ichthyosaurs have a broad interclavicle, which is more triangular in outline than the attenuated T-shape of other ichthyosaurs. The anterior flange of the humerus is seen well in several mixosaurid taxa, where the large development of this flange can extend the radial facet anteriorly greatly, for example in *Mixosaurus xindianensis* Chen & Cheng, 2010 and *Mixosaurus cornalianus* (Reposi 1902). The constricted diaphysis of the humerus is reduced in mixosaurids, and the epipodials become shorter, relative to the humerus (Reposi 1902; Schmitz *et al.* 2004). The metacarpals of mixosaurid ichthyosaurs are more homogeneous in form than in other ichthyosaurs: slightly elongate, with a minor median constriction, and an overall quadrate shape (Reposi 1902; Wiman 1912). The phalanges in mixosaurids have a square outline and slight evidence of a diaphysis (Reposi 1902; Chen & Cheng 2010). The femur, and the hindlimb generally, is not much smaller than the forelimb; it is strongly reduced in more derived taxa (Reposi 1902; Brinkmann 1996; McGowan & Motani 2003). Distally, the tibia articulates with three elements, while the fibula articulates with two; the astragalus is inserted

between the two epipodials distally, and the fibula is deflected posteriorly by its articulation with the femur (Repossi 1902; Wiman 1910).

Basal Merriamosauria. This grouping of non-neoichthyosaurian merriamosaurians (*sensu* Motani 1999b and Motani *et al.* 2015a) includes several taxa that can be informally termed ‘shastasaur-grade’, forming the more derived portion of Motani’s (2005c) intermediate grade. They represent most late Middle–Late Triassic taxa, and share similarities in their cranial and forelimb osteology. Taxa within this group include *Besanosaurus leptorhynchus* Dal Sasso & Pinna, 1996, *Californosaurus perrini* Merriam, 1902, *Callawayia neoscapularis* (McGowan, 1994a), *Guanlingsaurus liangae* Yin in Yin *et al.*, 2000, *Guizhouichthyosaurus* Cao & Luo in Yin *et al.*, 2000, *Qianichthyosaurus* Li, 1999, *Shastasaurus* Merriam, 1895, *Shonisaurus popularis* Camp, 1976, and *Toretocnemus* Merriam, 1903.

An unusual supranarial crest is present in *Qianichthyosaurus zhoui* Li, 1999 that extends mediolaterally on the external surface of the nasal (Nicholls *et al.* 2003; Maisch *et al.* 2008a). Maisch *et al.* (2008a) suggested a relationship between this and the anterior terrace of the supratemporal fenestra, but questioned this as there is no development of a sagittal ridge. Posterior to this, the unusual shortness of the posterior nasals in *Qianichthyosaurus zhoui*, *Qianichthyosaurus xingyiensis* Ji, Jiang & Motani in Yang *et al.*, 2013, and the mixosaurid *Phalarodon atavus*, among others, allows for an extensive contact between the lateral frontal and prefrontal (Maisch *et al.* 2008a; Liu *et al.* 2013; Yang *et al.* 2013). The parietal in *Shonisaurus popularis* has a simpler, straighter form than *Ophthalmosaurus icenicus* and *Brachypterygius extremus*, without the posterolateral deflection of the supratemporal process (Camp 1980, pp. 152–153, fig. 4). The parietal also has a much greater contribution to the pineal foramen in *Shonisaurus popularis* than in *Ophthalmosaurus icenicus*. *Shonisaurus*

popularis and *Cymbospondylus petrinus*, along with the mixosaurids *Phalarodon atavus* and *Mixosaurus cornalianus* (see below), show strong development of a high sagittal crest that runs along the midline of the parietals, frontals, and nasals (Huene 1949a; Motani 1999c; Maisch & Matzke 2000a). This marks the medial margin of the anterior terrace of the supratemporal fenestra in which the parietal has a large part (Motani 1999b, fig. 3). A longer and curved postorbital, similar to that found in *Ophthalmosaurus icenicus*, is seen in *Shastasaurus alexandrae*, *Macgowania janiceps* (McGowan, 1996a), and *Callawayia neoscapularis*, as well as possibly in *Hudsonelpidia brevirostris* McGowan, 1995 (Merriam 1902; Maisch 2000; Nicholls & Manabe 2001). These taxa, along with *Ichthyosaurus communis*, show only the crescentic postorbital rim, and not the posterior lamella found in *Ophthalmosaurus icenicus*. The palatine of *Shonisaurus popularis* shows broad, fan-like structures dorsally that Camp (1980) suggested were suture lines for the maxilla; the contact between the two may be more complex than the simple overlap seen in *Ophthalmosaurus icenicus*. The supraoccipital is only a minor participant in the *foramen magnum* in many Triassic ichthyosaurs, such as *Guizhouichthyosaurus tangae* Cao & Luo in Yin *et al.*, 2000 and *Cymbospondylus petrinus* (Merriam 1908; Maisch & Matzke 2004; Shang *et al.* 2012), but is more important in *Brachypterygius extremus* and *Ophthalmosaurus* (see discussion on the synonymy of *Ophthalmosaurus* and *Baptanodon* below). In basal merriamosaurians, the bones of the occipital region are more massive and have closer contact than in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. For example, the stapes in *Shonisaurus popularis*, *Guizhouichthyosaurus tangae*, and *Besanosaurus leptorhynchus* is composed of a massive, flattened footplate that abutted against the lateral face of the basioccipital and a much more slender distal portion that extended towards the quadrate (Camp 1980; Shang *et al.* 2012). The dentary in *Guanlingsaurus liangae*, along with the premaxilla and maxilla, does not have an alveolar groove, supporting the view that this taxon,

and the genus more generally, was edentulous (Maisch 2000; Sander *et al.* 2011; Ji *et al.* 2013; Motani *et al.* 2013). Unlike in *Ophthalmosaurus icenicus*, the parapophysis in ‘shastasaur grade’ taxa is not retained throughout the presacral column, but instead this facet is reduced posteriorly and lost posterior to centra 7–15, depending on the species (Merriam 1908; Sander 1989); the rib articulates with this single facet.

The humeri in *Shastasaurus* and *Shonisaurus* are modified to robust and broad, square elements by the expansion of the humeral diaphysis (Merriam 1908; Camp 1980). Many basal Merriamosauria have notching on elements of the fore and hind limbs. *Callawayia neoscapularis*, and *Toretocnemus zitteli* (Merriam, 1903) have closely fitting forelimb epipodials: the space between the radius and ulna is reduced to a foramen formed by two notches in their posterior and anterior margins respectively (Merriam 1903, 1905; Sander 1989; McGowan 1994a; Nicholls & Manabe 2001). The first metacarpal does not ossify in Merriamosauria (*sensu* Motani 1999b), resulting in the loss of the first digit distal to this, as shown in *Besanosaurus leptospondylus*, *Toretocnemus zitteli*, and Euichthyosauria (Merriam 1903, 1905; Dal Sasso & Pinna 1996). The additional digits of more derived ichthyosaurs are a neomorphic development that extend the limbs (Motani 1999a). There is further reduction of the number of digits in Shastasaurinae (*sensu* Motani 1999b) to three with the loss of the second metacarpal and supported digit (Camp 1980). The fifth digit in *Toretocnemus zitteli* also appears to be lost, or greatly reduced (Merriam 1903, 1905). The carpals are largely rounded in these Late Triassic ichthyosaurs, as in *Callawayia neoscapularis* (Nicholls & Manabe 2001), but are polygonal and more closely articulated in post-Triassic taxa. Rounded limb elements are apparently a convergent feature in *Ophthalmosaurus icenicus*. In *Besanosaurus leptorhynchus*, *Shastasaurus pacificus* Merriam, 1895, and *Californosaurus perrini*, the obturator foramen between the ischium and pubis is open, forming a notch on the posterior margin of the pubis (Merriam 1902; Dal Sasso & Pinna 1996). This distal notch

becomes fully enclosed in the basal parvipelvians *Hudsonelpidia brevirostris* and *Macgowania janiceps* by the proximal and distal contact of the pubis and ischium, although they are not fused (McGowan 1995, 1996a). *Callawayia neoscapularis* has a femur with a similar form to *Toretocnemus californicus* Merriam, 1903, with well-developed dorsal and ventral processes; particularly the dorsal process is developed into a prominent longitudinal ridge (Nicholls & Manabe 2001).

ACAMPTONECTES DENSUS FISCHER *ET AL.*, 2012

Acamptonectes is represented by a single valid species: *Acamptonectes densus* Fischer *et al.*, 2012 from the Speeton Clay Formation (Hauterivian) of North Yorkshire, United Kingdom, and Lower Saxony, Germany. *Acamptonectes densus* is recovered within a paraphyletic *Ophthalmosaurus* (sister to *Ophthalmosaurus natans*) by Fischer *et al.* (2012) and Fischer *et al.* (2013), so is one of the closest relatives to *Ophthalmosaurus icenicus*. This taxon is represented by few remains that poorly preserve much of the body, but its similarity to *Ophthalmosaurus icenicus* warrants discussion.

The anterior portion of the skull in *Acamptonectes densus* is disarticulated and incomplete (Fischer *et al.* 2012). The quadrate condyle of *Acamptonectes densus* is angled more medially and extends farther dorsally on the quadrate than in either *Brachypterygius extremus* or *Ophthalmosaurus icenicus*, a trait shared with some species of *Platypterygius* and *Ophthalmosaurinae* indet. (Kolb & Sander 2009; Adams & Fiorillo 2011; Fischer *et al.* 2012; Druckenmiller & Maxwell 2014). The basiptyergoid processes of *Acamptonectes densus* are much larger than in either *Brachypterygius extremus* or *Ophthalmosaurus icenicus*, although they are not as clearly separated from the main body of the basisphenoid as in *Brachypterygius extremus* (Text-fig. 41; Pl. 33, figs 1–4, Pl. 34, figs 1–4). Similarly, the dorsal basisphenoid of *Acamptonectes densus* is developed into a medial sagittally-aligned

crest that is autapomorphic. The membranous labyrinth is particularly well defined on the posterior surface of the prootic of *Acamptonectes densus*: the impression of the horizontal semicircular canal extends to the lateral margin, without the cartilage-covered border found in *Ophthalmosaurus icenicus*. Additionally, a rounded process extends medially from the dorsomedial margin that is interpreted as origin of the *M. adductor mandibulae externus* (Fischer *et al.* 2012), which is reduced in *Ophthalmosaurus icenicus* to an anterior ridge ventrally (Text-fig. 11; Pl. 8, figs 1, 2 in Part 1). The extracondylar area of the basioccipital in *Acamptonectes densus* is narrower than in *Ophthalmosaurus icenicus* and shares small ventral tubers separated by a notch. However, the extracondylar area is not as reduced as in *Brachypterygius extremus*, which does not share that ventral notch. Further, the floor of the foramen magnum in *Acamptonectes densus* is divided sagittally by a low ridge not found in any other taxon. The medial shaft of the stapes of *Acamptonectes densus* is more slender than in *Ophthalmosaurus icenicus*, and the medial head is cubic in shape *Acamptonectes densus* (an autapomorphy; Fischer *et al.* 2012) rather than the more rounded, bulbous form in *Ophthalmosaurus icenicus*. *Acamptonectes densus* shows variability in the processes anterior to the jaw articulation on the surangular: the paracoronoid process is always present, but the preglenoid process is not always present (Fischer *et al.* 2012).

The margins of the anterior and posterior faces of the centra in *Acamptonectes densus* bulge slightly, interlocking between centra to form a stiff axis (Fischer *et al.* 2012). There are no grooves on the anterior or posterior faces of the ribs in *Acamptonectes densus*, whereas there are in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, so the rib has a rounded cross-section (Fischer *et al.* 2012). This is similar to the distal rib portions in *Nannopterygius enthekiodon*, although this taxon has a median groove proximally. Proximally, the scapula of *Acamptonectes densus* is broader than in *Brachypterygius extremus* (Pl. 37, figs 14, 15), with the strong development of the acromion process found in

some specimens of *Ophthalmosaurus icenicus*. The humerus of *Acamptonectes densus* shares the distal facet configuration of *Ophthalmosaurus icenicus* (articulating with the anterior accessory element, radius, and ulna). Unlike in *Ophthalmosaurus icenicus*, the anteriormost facet is crescentic in *Acamptonectes densus*, so that the anterodistal margin of the humerus is rounded rather than angled (Text-fig. 33; Pl. 23, fig. 6 in Part 1). As in *Ophthalmosaurus icenicus*, and unlike most other neoichthyosaurs, the posterior margin of the ulna in *Acamptonectes densus* is concave and edgy, rather than being almost as thick of the rest of the element (Fischer *et al.* 2012, character 36). Furthermore, the ulna in *Acamptonectes densus* has a small posterior facet distally that is found in *Ophthalmosaurus icenicus* (Text-fig. 33g in Part 1), but is much smaller than the facet for the post-axial accessory element in *Brachypterygius extremus* (Text-fig. 42a; Pl. 38, fig. 4).

AEGIROSAURUS LEPTOSPONDYLUS (WAGNER, 1853)

Aegirosaurus leptospondylus (Wagner, 1853) is known from the Solnhofen Formation (Tithonian) of Bavaria, Germany. Originally described as *Ichthyosaurus leptospondylus* Wagner, 1853, the genus *Aegirosaurus* was erected by Bardet & Fernández (2000). Recent phylogenetic analyses have placed *Aegirosaurus leptospondylus* within Platypterygiinae, as sister to *Sveltonectes insolitus* and close to *Brachypterygius extremus* (Fischer *et al.* 2012; Fischer *et al.* 2013; Roberts *et al.* 2014; Arkhangelsky & Zverkov 2014).

The maxilla in *Aegirosaurus leptospondylus* has much less extensive lateral exposure than in *Brachypterygius extremus* as the jugal does not extend so far anterior as in the latter species, restricting this, which is more similar to *Ophthalmosaurus icenicus* (Text-figs 4a [in Part 1], 39). However, the contact between the premaxilla and lachrymal is more extensive in *Aegirosaurus leptospondylus* than in *Ophthalmosaurus icenicus*, similar to *Brachypterygius extremus*, so that the maxilla is clearly separated from the external naris. The postorbital

region is narrower in *Aegirosaurus leptospondylus* than in CAMSM J68516 (Text-fig. 37), and more similar to *Ophthalmosaurus icenicus* as the postorbital covers much of the quadratojugal: there is greater exposure of the quadratojugal in *Brachypterygius extremus*. In *Aegirosaurus leptospondylus*, the snout is not as robust as in *Brachypterygius extremus*, and the dentition is reduced, as is found in both *Nannopterygius enthekiodon* and *Ophthalmosaurus icenicus*. The neotype specimen SM of *Aegirosaurus leptospondylus* does have a more elongate snout than any of the ichthyosaurs described above, but the development of this appears to be variable (Bardet & Fernández 2000).

Unlike in both *Nannopterygius enthekiodon* and *Ophthalmosaurus icenicus*, the posterior presacral–anterior caudal vertebrae of *Aegirosaurus leptospondylus* do not increase in height in this region. Additionally, Bardet & Fernández (2000, p. 507) describe posteriorly recurved neural arches in the presacral region, with large neural canals. In *Aegirosaurus leptospondylus*, the humerus has a similar configuration of humeral facets to *Brachypterygius extremus* (articulating with the radius, intermedium, and ulna respectively). Distally, the humerus of *Aegirosaurus leptospondylus* is not expanded so far anteroposteriorly as in *Brachypterygius extremus* or *Ophthalmosaurus icenicus*: the proximal and distal widths are subequal in *Aegirosaurus leptospondylus*. The forelimbs of *Aegirosaurus leptospondylus* contain many more elements than have been found for *Brachypterygius extremus*, *Nannopterygius enthekiodon*, or *Ophthalmosaurus icenicus*: up to 20 in a single digit, whereas the maximum known for the other taxa are 16, four, and nine respectively. Similarly, the post-axial digits of both *Aegirosaurus leptospondylus* and *Brachypterygius extremus* are important and better developed than in *Ophthalmosaurus icenicus*.

ARTHROPTERYGIUS MAXWELL, 2010

Ophthalmosaurus chrisorum Russell, 1993 was described from the Ringnes Formation (Oxfordian–Kimmeridgian) of Melville Island, Northwest Territories, Canada; this material was later assigned to the new taxon *Arthropterygius* Maxwell, 2010 (see also the generic discussion of *Ophthalmosaurus* in Part 1). The material referred to this taxon includes basicranial, vertebral, pectoral and forelimb, and pelvic and hindlimb elements (Maxwell 2010). Additional material has been referred to *Arthropterygius* sp. by Fernández & Maxwell (2012) from the Vaca Muerta Formation (Tithonian) of Neuquén Province, Argentina, and by Zverkov *et al.* (2015) from the Paromes Formation (Tithonian) of Sosnogorsk District, Komi Republic, Russia, which will also be considered here. *Arthropterygius chrisorum* is typically found as the most basal member of Ophthalmosauridae following Fischer *et al.*'s (2011, p. 1020) definition (Fischer *et al.* 2012; Fischer *et al.* 2013; Roberts *et al.* 2014; Arkhangelsky & Zverkov 2014), but has been recovered in a more derived position within Ophthalmosauridae (Maxwell 2010; Druckenmiller & Maxwell 2010).

The basisphenoid of *Arthropterygius* has a similar morphology to *Ophthalmosaurus icenicus*. Like in *Brachypterygius extremus*, the ventral entrance of the internal carotid foramen is positioned more posteriorly in *Arthropterygius* than in *Ophthalmosaurus icenicus*, but in *Arthropterygius*, this foramen is positioned further posteriorly in the posteriormost face of the basisphenoid with a recessed area ventral to the passage of the foramen on the ventral surface that is not found in the taxa described above. The basipterygoid processes are not so well differentiated from the main body of the basisphenoid in *Arthropterygius* as in either *Brachypterygius extremus* or *Ophthalmosaurus icenicus*, although posteriorly they are demarcated by a groove for the facial (VII) nerve (Maxwell 2010). Anteriorly, the basioccipital of *Arthropterygius* has a raised, square boss for articulation with the basisphenoid that is similar to *Ophthalmosaurus icenicus*, although more clearly offset from

the main body of the basioccipital, but not found in *Brachypterygius extremus*. Like in both *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, some specimens of *Arthropterygius* preserve a well-defined notochordal pit dorsally on the anterior face. In posterior view, the extracondylar area of the basioccipital in *Arthropterygius* is not exposed so prominently as in *Ophthalmosaurus icenicus*, but is more extensive than in *Brachypterygius extremus*.

The pectoral elements of *Arthropterygius* show great similarity to *Ophthalmosaurus icenicus* (Maxwell 2010). The humerus of *Arthropterygius* is differentiated from both *Brachypterygius extremus* and *Ophthalmosaurus icenicus* by the relatively smaller dorsal and ventral processes proximally; the ventral process is particularly poorly developed relative to more derived ophthalmosaurids. Distally, the humeral facets of *Arthropterygius* match the configuration of *Ophthalmosaurus icenicus*, however, the ulnar facet is not so greatly deflected posteriorly in *Arthropterygius* and has a pronounced ventral torsion. The manual pre-axial accessory element in *Arthropterygius* is rounded rather than teardrop-shaped as it is in *Brachypterygius extremus*. Similar to the humerus, the dorsal and ventral processes on the femur of *Arthropterygius* are poorly demarcated from the main body and not so well developed compared to *Ophthalmosaurus icenicus*, and distally, the tibial facet is much larger than the fibular facet in *Arthropterygius*.

ATHABASCASAURUS BITUMINEUS DRUCKENMILLER & MAXWELL, 2010

Athabascasaurus bitumineus Druckenmiller & Maxwell, 2010 is known from a single specimen from the Wabiskaw Member of the Clearwater Formation (Albian) of a locality ~35 km north of Fort Murray, Alberta, Canada. The specimen is preserved in dorsal view, and much of the girdles, limbs, anterior snout, and the end of the tail are either not easily visible or missing (Druckenmiller & Maxwell 2010). Because of this, *Athabascasaurus*

bitumineus has been difficult to place phylogenetically, and has been resolved within Platypterygiinae as sister to *Platypterygius australis* (Fischer *et al.* 2012; Fischer *et al.* 2014b; Arkhangelsky & Zverkov 2014), within Ophthalmosaurinae as sister to a Svalbard ichthyosaur-containing clade (Roberts *et al.* 2014), or within a ladderized Ophthalmosauridae that is approximately equal to a paraphyletic Ophthalmosaurinae (Druckenmiller & Maxwell 2010).

In *Athabascasaurus bitumineus*, the premaxilla reaches posteriorly to form part of the margin of the external naris as is found in other ichthyosaurs; this is interpreted from the premaxillary facets on the maxilla (Druckenmiller & Maxwell 2010, fig. 6). The pineal foramen of *Athabascasaurus bitumineus* is anteroposteriorly elongate, and only surrounded anteriorly by the frontals, the posterior portion being bordered by the parietals; in *Ophthalmosaurus icenicus*, the frontals surround almost the entirety of the smaller pineal foramen. Additionally, the frontals of *Athabascasaurus bitumineus* have a smaller exposure dorsally than in *Ophthalmosaurus icenicus*, excluded mostly by what is likely a medial extension of the postfrontal. The squamosal of *Athabascasaurus bitumineus* is square, similar to *Caypullisaurus bonapartei* (Fernández 2007a), not triangular as found in *Ophthalmosaurus icenicus* (Pl. 4, figs 1, 2 in Part 1). Like in *Ophthalmosaurus icenicus*, the atlas and axis of *Athabascasaurus bitumineus* are fused, but do not have a clear suture line along this fusion; the diapophyses and parapophyses are fused on the atlas-axis. The ilium of *Athabascasaurus bitumineus* is strongly posteriorly curved proximally, more than in *Ophthalmosaurus icenicus*, and the ischiopubis of the former taxon does not possess an obturator foramen, nor partly defined suture line seen in the latter taxon.

CRYOPTERYGIUS KRISTIANSENAE DRUCKENMILLER *ET AL.*, 2012

Cryptopterygius kristiansenae Druckenmiller *et al.*, 2012 is known from a single specimen from the Sløttsmoya Member of the Agardhfjellet Formation (Tithonian) of Spitsbergen, Svalbard; the specimen is largely complete and preserved in lateral view. Roberts *et al.* (2014) found this taxon to be within Ophthalmosaurinae in a Svalbard ichthyosaur-polytomy, while Arkhangelsky & Zverkov (2014) found *Cryptopterygius kristiansenae* to be in a polytomy within their Ophthalmosaurinae alongside *Ophthalmosaurus icenicus*, *Ophthalmosaurus natans*, *Acamptonectes densus*, *Undorosaurus gorodischensis*, and *Paraophthalmosaurus*.

In *Cryptopterygius kristiansenae*, the posterior margin of the lachrymal is angled ventrally, creating a near 90° bend in the anterior margin of the orbit, rather than the more continuous curve seen in the British taxa described above. The postorbital exposure is anteroposteriorly longer in *Cryptopterygius kristiansenae* than in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, but this may be due in part to disarticulation in this region; together the postorbital region is longer than in *Nannopterygius enthekiodon* and *Ophthalmosaurus icenicus*, and more similar to *Brachypterygius extremus*. The presacral region of *Cryptopterygius kristiansenae* contains 52 vertebrae, more than the 42 of *Nannopterygius enthekiodon* and 39–42 of *Ophthalmosaurus icenicus*, but this is determined based upon the position of the ilium rather than the rib articulations in *Cryptopterygius kristiansenae*.

The transverse bar of the interclavicle in *Cryptopterygius kristiansenae* is longer than the median stem, which is strongly broadened distally, becoming spatulate, which is not the case in *Ophthalmosaurus icenicus* (Text-fig. 31; Pl. 20, fig. 1, 2 in Part 1). The coracoid is square posteriorly in *Cryptopterygius kristiansenae* rather than the rounded form of *Ophthalmosaurus icenicus* or the transversely-angled posterior margin found in *Brachypterygius extremus* and

Nannopterygius enthekiodon. Unlike both *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, the humerus of *Cryptopterygius kristiansenae* has only two distal facets, articulating with the radius and ulna. This is similar to *Macropterygius* described and discussed above, and *Nannopterygius enthekiodon*, although the distal humeral facets in *Cryptopterygius kristiansenae* are approximately equal in size, whereas in the latter taxon the ulnar facet appears to be larger. Distal to the humerus, the limb elements in *Cryptopterygius kristiansenae* are mostly polygonal, as in *Brachypterygius extremus*, but are thickened like in *Ophthalmosaurus icenicus*. The ilium in *Cryptopterygius kristiansenae* is broader distally and more flattened than in *Ophthalmosaurus icenicus*. Further, the ischium is not fused distally to the pubis, so does not form an obturator foramen, as in *Ophthalmosaurus icenicus* (Text-fig. 35a, b; Pl. 24, figs 3–8 in Part 1).

DEARCMHARA SHAWCROSSI BRUSATTE ET AL., 2015

Dearcmhara shawcrossi Brusatte et al., 2015 is known from associated partial distal humerus and three vertebrae likely from the Bearreraig Sandstone Formation (late Toarcian–late Lower Bajocian) of the Isle of Skye, United Kingdom. Its recent description and the uncertainty of its dating means that it was not included in the systematic palaeontology above (although see the discussion on Neoichthyosauria). It was assigned to the clade Neoichthyosauria by Brusatte et al. (2015) based upon a waisted humerus and prominent anterodistal leading edge; the humerus resembles other ‘leptonectid’ ichthyosaurs, both Leptonectidae and *Temnodontosaurus*, in this. Distally, the humerus possesses two large facets, but unlike *Nannopterygius enthekiodon*, has a small facet on the leading edge of the anterodistal prominence, with the concavity of this being an autapomorphy of *Dearcmhara shawcrossi*. The presence of a large supraulnar process is found in *Ophthalmosaurus icenicus* as well as *Dearcmhara shawcrossi*, but is variably developed in the former taxon. Similarly,

concavities in the dorsal and lateral profile of the ulnar facet of *Dearcmhara shawcrossi* are also found in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*.

LEPTONECTIDAE MAISCH, 1998a

Leptonectidae Maisch, 1998a (last common ancestor of *Eurhinosaurus longirostris* and *Leptonectes tenuirostris*) is united by several features of the snout, postorbital skull, and limbs (Motani 1999b; Sander 2000; Maisch & Matzke 2000). This clade of Early Jurassic ichthyosaurs is known from the Lias Group (Hettangian–Pliensbachian) of the south-western United Kingdom, and the Posidonia Shale Formation (Toarcian) of south-western Germany (Maisch & Matzke 2000; McGowan & Motani 2003). Within Leptonectidae are typically: *Eurhinosaurus longirostris* (Mantell, 1851), *Excalibosaurus costini* McGowan, 1986, and three species of *Leptonectes* McGowan, 1996b. *Temnodontosaurus* was recovered as the sister to Leptonectidae by Fischer *et al.* (2013), however, Leptonectidae was recovered as paraphyletic by Maxwell *et al.* (2012b).

One of the most compelling features of *Eurhinosaurus longirostris* is the elongation of the premaxilla relative to the skull and lower jaw. The premaxilla comprises around 77% of the length of the skull in *Eurhinosaurus longirostris* and 68% in *Excalibosaurus costini* (McGowan 1986), much greater than in *Brachypterygius extremus*, *Ophthalmosaurus icenicus*, or *Nannopterygius enthekiodon*. As the full elongation that is characteristic of *Eurhinosaurus longirostris* and *Excalibosaurus costini* is limited to the premaxilla, these taxa do not show a corresponding elongation of the dentary (McGowan 1986). Relative shortening of the mandible is also found in *Leptonectes* and *Temnodontosaurus*, but to a much lesser extent (Motani 1999b; Maisch & Matzke 2000; McGowan & Motani 2003). In *Leptonectes tenuirostris* (Conybeare, 1822), the parietal ridge is well developed and this is accompanied by a large parietal shelf posteriorly, similar to *Stenopterygius triscissus*, but unlike in

Brachypterygius extremus and *Ophthalmosaurus icenicus* (Owen 1881; Huene 1922b; Godefroit 1993b, 1995; Maisch & Matzke 2003). Unlike other neoichthyosaurians, the supratemporal fenestra is greatly reduced in size in the leptonectids *Eurhinosaurus longirostris*, to a lesser degree *Leptonectes tenuirostris*, but also in the ecologically convergent *Hauffiopteryx typicus* (Huene 1928, 1951; Maisch & Matzke 2003; Maisch 2008). This is, at least partially, a result of the anteroposterior shortening of the postorbital region, which largely becomes posteriorly-directed in these taxa (Motani 1999b). The extent of the supratemporal in *Leptonectes* cf. *tenuirostris* is similar to *Ophthalmosaurus icenicus*, especially the ventral ramus, which extends ventrally to the pterygoid in both taxa, and has a clear protuberance that likely indicates a main area for attachment of the *M. depressor mandibulae* (Text-fig. 16a; Pl. 2, fig. 6 in Part 1; Maisch & Matzke 2003, fig. 4). Unlike in *Ophthalmosaurus icenicus*, there is no horizontal shelf dorsal to the opisthotic facet on the supratemporal in *Leptonectes tenuirostris* (Maisch & Matzke 2003); this is also the case in *Ichthyosaurus communis* and *Stenopterygius triscissus* (Owen 1881; McGowan 1973a; Godefroit 1994). In *Eurhinosaurus longirostris*, the supraoccipital is visible posteroventrally to the parietals, whereas in *Brachypterygius extremus*, *Ophthalmosaurus icenicus*, and *Stenopterygius triscissus* the parietals cover the supraoccipital dorsally (Huene 1949b). Mazin (1988) and Godefroit (1993b) described *Leptonectes tenuirostris* and ‘*Stenopterygius longifrons*’ (Owen, 1881) (= *Stenopterygius triscissus*) with three facets on the quadrate condyle that articulate with the articular and the surangular. Many Lower Jurassic ichthyosaurs have stapes with a shorter lateral shaft than in *Ophthalmosaurus icenicus*, for example, *Temnodontosaurus azerguensis*, *Leptonectes tenuirostris* and *Eurhinosaurus longirostris* (Huene 1928, 1951; Lomax & Massare 2012; Martin *et al.* 2012). Unlike in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, *Leptonectes* cf. *tenuirostris* shares a marked ventral notch in the postorbital region with the Triassic taxa *Cymbospondylus*

petrinus and *Phalarodon atavus* (Merriam 1908; McGowan 1974b; Motani 1999c; Maisch & Matzke 2000a, 2001, 2003, 2004). The dentary of *Eurhinosaurus longirostris* is very low, corresponding to its reduced size, giving its mandible a generally gracile form (Reisdorf *et al.* 2011). The articular surface in *Leptonectes tenuirostris* and *Eurhinosaurus longirostris* is larger than in *Ophthalmosaurus icenicus*, with well-defined facets proximally (Owen 1881; Huene 1928, 1951).

The humerus of *Leptonectes* does not have either a strongly developed dorsal or ventral process proximally, and is anteroposteriorly expanded distally. Anterodistally, the humerus of *Leptonectes* has a rounded prominence that is not found in thunnosaurian ichthyosaurs (McGowan & Milner 1999; McGowan & Motani 2003; Fischer *et al.* 2013). Anterior notches on the radius are not present in any of the taxa described above, but are found in *Leptonectes tenuirostris*, *Macgowania janiceps*, and *Stenopterygius quadriscissus*, among others (McGowan 1991, 1996a; Motani 1999a; Maisch 2008). The relative size of metacarpal five compared to various other mesopodial elements, particularly distal carpals one and four is also regarded as an important feature (e.g. Maisch & Matzke 2000, character 100). In some Liassic taxa, such as *Leptonectes* (McGowan 1991; McGowan & Milner 1999), the fourth distal carpal is larger than the fifth metacarpal. The ischium and pubis are also more equally sized in *Leptonectes solei* (McGowan, 1993), but the pubis is larger, as in *Ichthyosaurus breviceps* whereas the opposite is the case in *Ophthalmosaurus icenicus* (Lomax 2010). In *Leptonectes*, the ischium and pubis are expanded and fused distally, and proximally in some cases (Lomax & Massare 2012).

HAUFFIOPTERYX TYPICUS MAISCH, 2008

Hauffiopteryx typicus Maisch, 2008 was erected to hold part of the material that had previously been referred to *Stenopterygius hauffianus* Huene, 1922b (Maisch 2008; Maxwell

2012a, fig. 1). This taxon is known from the Posidonia Shale Formation (Toarcian) of south-western Germany (Maisch 2008), and further specimens have been referred from the Strawberry Bank Locality, Upper lias (Toarcian) of south-western United Kingdom, but assignment of these has been questioned (Caine & Benton 2011; Marek *et al.* 2015). *Hauffiopteryx typicus* is a neoichthyosaurian ichthyosaur, usually positioned close to or within Thunnosauria (Caine & Benton 2011; Maxwell *et al.* 2012b; Fischer *et al.* 2013; Marek *et al.* 2015), but has also been found as the sister taxon to Leptonectidae (Caine & Benton 2011).

The premaxilla in *Hauffiopteryx typicus* does not possess a supranarial process, and only forms a small part of the ventral border of the anterior external naris, unlike in *Brachypterygius extremus* and *Ophthalmosaurus icenicus* (Maisch 2008; Caine & Benton 2011; Marek *et al.* 2015). The short postorbital region and reduced supratemporal fenestra in *Hauffiopteryx typicus* is similar to members of Leptonectidae, particularly *Leptonectes* (see below), and has led to suggestions of an affinity between these taxa (Caine & Benton 2011). However, this may be due to ecological convergence with Leptonectidae as more recent phylogenies recover *Hauffiopteryx typicus* within the more derived Thunnosauria (Martin *et al.* 2012; Fischer *et al.* 2013). The quadrate of *Hauffiopteryx typicus* does not have an occipital lamella dorsally, unlike in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. The quadrate condyle is neither offset nor as large in *Hauffiopteryx typicus* as in these two taxa either (Marek *et al.* 2015). The size of the paroccipital process of the opisthotic in *Hauffiopteryx typicus* differs from other neoichthyosaurians (Fischer *et al.* 2012, character 20): it is short and robust, without being offset from the main body of the opisthotic (Caine & Benton 2011; Marek *et al.* 2015). The extracondylar area of the basioccipital in *Hauffiopteryx typicus* is reduced compared to *Ichthyosaurus* and *Temnodontosaurus*, but is

larger than in *Ophthalmosaurus icenicus*, and the ventral tubers are broader and more widely separated (Marek *et al.* 2015).

The transverse bar of the interclavicle in *Hauffiopteryx typicus* is pointed distally: a flange of bone joins the two arms of the T of the interclavicle, which is not found in *Ophthalmosaurus icenicus* (Caine & Benton 2011). Proximally, the scapula of *Hauffiopteryx typicus* does not have an enlarged and separate acromion process, as in the Baracromia (Maisch 2008; Caine & Benton 2011). Like in *Stenopterygius* below, and unlike in Ophthalmosauridae, the humerus of *Hauffiopteryx typicus* does not have a large, demarcated dorsal process on the humerus, but does retain a large ventral process that extends more than half of the length of the humerus (Caine & Benton 2011). The ischiopubis is unfused distally in *Hauffiopteryx typicus*: the ischium is narrower than the pubis, but the pubis becomes broader proximally and distally (Maisch 2008; Caine & Benton 2011). The femur in *Hauffiopteryx typicus* is expanded distally, and the anterior margin of the leading edge elements in the hindlimb are notched (Caine & Benton 2011); in *Ophthalmosaurus icenicus*, the distal femur is narrower, and notching is not present.

ICHTHYOSAURUS KÖNIG, 1818

The taxonomy of *Ichthyosaurus* König, 1818 has been problematic and is currently the topic of revision. Between four and six species are currently referred to *Ichthyosaurus* of which *Ichthyosaurus communis* Conybeare, 1822, *Ichthyosaurus breviceps* Owen, 1881, *Ichthyosaurus conybearei* Lydekker, 1888, and *Ichthyosaurus anningae* Lomax & Massare, 2015 are generally considered to be valid members (McGowan & Motani 2003; Cleary *et al.* 2015; Lomax & Massare 2015). Maisch (1997b, 2010, p. 166) and Maisch & Matzke (2000, p. 74) considered *Ichthyosaurus intermedius* Conybeare, 1822 to be a separate valid species, however, recent studies have typically incorporated the relevant material into *Ichthyosaurus*

communis (McGowan 1974b; McGowan & Motani 2003; Lomax & Massare 2015).

Additionally, Maisch (2010, p. 165) has also separated '*Ichthyosaurus*' *acutirostris* Owen, 1840 as potentially representing a separate genus. The first five species of *Ichthyosaurus* detailed above are known from the Lias Group (Hettangian–Pliensbachian) of Dorset and Somerset, United Kingdom (McGowan 1974b; Bennett *et al.* 2012; Lomax & Massare 2015), while '*Ichthyosaurus*' *acutirostris* is known from the Alum Shale Formation (Toarcian) of Whitby. Because of these taxonomic issues, comparisons will mostly be drawn between the first four species of *Ichthyosaurus* listed above that are accepted as valid; with the most material available, *Ichthyosaurus communis* will be compared to most extensively.

In *Ichthyosaurus communis*, the vomer is excluded from ventral view anteriorly as the ventromedial margins of the two premaxilla meet (Sollas 1916; McGowan 1973a), whereas in *Ophthalmosaurus icenicus*, the vomer is exposed ventrally for its entire length (Text-fig. 5b in Part 1). Like in *Palvennia hoybergeti* below, the premaxilla of *Ichthyosaurus breviceps* is much shorter than in *Brachypterygius extremus*, *Ophthalmosaurus icenicus*, or *Nannopterygius enthekiodon* at only 49% of the skull length (McGowan 1974b). The posterior portion of the premaxilla and nasal in *Ophthalmosaurus icenicus* is squarer in cross section than in *Ichthyosaurus communis*, and this is stronger still in *Brachypterygius extremus*: the premaxillae and nasals have a greater angular displacement between their dorsal and lateral surfaces (Sollas 1916; McGowan 1973a, 1976; Kirton 1983). The supranarial process of the premaxilla in *Ichthyosaurus communis* extends for the full length of the external naris, whereas in *Ophthalmosaurus icenicus*, the supranarial process is only one-half of the length of the external naris (Owen 1881; McGowan 1974b; McGowan & Motani 2003). On the maxilla, the bony ridge that forms the ventral margin of the lachrymal facet is not as well developed in *Ophthalmosaurus icenicus* as in *Ichthyosaurus* (this region is not visible in *Brachypterygius extremus*), and the latter lacks the posterodorsal palatal

processes seen in *Ophthalmosaurus icenicus*, having medial fenestrations instead (McGowan 1973a). Sollas's (1916) serial sections of *Ichthyosaurus* aff. *communis* show the great anterior extent of the nasals and that, posteriorly, the nasals meet at the midline with a tongue and groove suture that is not present in *Ophthalmosaurus icenicus* (e.g. Home 1820, pl. 16; Sollas 1916, fig. 2(10), sections 288 and 296). Around and posterior to the external naris, the nasals also show a lower lateral wall that is not at as great an angle to the dorsal wall as in *Brachypterygius extremus* or *Ophthalmosaurus icenicus*, and here a small facet for the lachrymal can be seen in *Ichthyosaurus communis* that is not present on the other taxa (McGowan 1973a). Unlike the taxa described above, *Ichthyosaurus communis*, *Stenopterygius triscissus* and *Sveltonectes insolitus* possess an internasal foramen, variably developed and usually located entirely between the nasals, posterior to the external naris (McGowan 1973a; Godefroit 1993b; Fischer *et al.* 2011). The lachrymal of *Ophthalmosaurus icenicus* differs markedly from *Ichthyosaurus communis* in its anterior extent, bordering only the posterior margin of the external naris in the latter species (Owen 1881; McGowan 1973a). The shortness of the lachrymal in *Ichthyosaurus communis* allows the maxilla to contact the external naris in external view. In *Ichthyosaurus intermedius*, the lachrymal extends ventrally along much of the external naris, forming interdigitating suture with the premaxilla that excludes the maxilla from the external naris (Maisch 1997b), rather than the simple overlap that is seen in *Ophthalmosaurus icenicus*. The prefrontal of *Ophthalmosaurus icenicus* resembles that of *Ichthyosaurus communis*, but in the latter species, this does not have as elongate an anterior extension (McGowan 1973a, 1974b). This prevents the prefrontal from being included in the external narial opening, and this state is observed in many other Liassic taxa, for example, *Temnodontosaurus platyodon*, *Temnodontosaurus trigonodon*, and *Leptonectes tenuirostris* (Owen 1881; McGowan 1974a, b; Maisch & Hungerbühler 2001; Maisch & Matzke 2003). Motani (2005a) showed that the prefrontal has a greater dorsal

exposure than was previously thought in *Stenopterygius* and *Ichthyosaurus*, contacting the frontals along their lateral margin. Unlike the rectangular frontal of *Ophthalmosaurus icenicus*, the frontal of *Ichthyosaurus communis* is more crescentic and has a narrower (laterally) dorsal exposure on the skull roof (Owen 1881; Sollas 1916; McGowan 1973a; Motani 2005a). *Ichthyosaurus* aff. *communis* also shows that the entirety of the pineal foramen was enclosed by the frontals.

While similar to the parietal of *Ophthalmosaurus icenicus* and *Brachypterygius extremus*, in *Ichthyosaurus* aff. *communis*, the two ventral processes on the parietal – lateral and medial – are more strongly developed: the lateral process is found in a smaller form in *Ophthalmosaurus icenicus* (Text-fig. 5a; Pl. 3 in Part 1), while the medial process is absent. *Ichthyosaurus* aff. *communis* possesses an ossified epipterygoid, which contacts the lateral ventral process of the parietal (Sollas 1916, fig. 2(5), section 453; McGowan 1973a); this element is not ossified in *Ophthalmosaurus icenicus* (see also *Platypterygius* below). The parietal of *Ichthyosaurus* aff. *communis* has a medial process that descends from the transverse ridge on the ventral surface meets the medial facet with the contralateral parietal. McGowan's (1973a) material shows that this forms a small transverse plate that he termed the parietal flange. Neither *Ophthalmosaurus icenicus* nor *Brachypterygius extremus* has a parietal ridge posteriorly that is as strongly developed as *Ichthyosaurus communis* or *Stenopterygius triscissus* (Owen 1881; Godefroit 1993b, 1995). The anterior portion of the postfrontal of *Ichthyosaurus* cf. *communis* is Y-shaped compared to the more rounded form of *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, and makes a smaller contribution to the dorsal skull roof in the former species due to more extensive overlap by the supratemporal (McGowan 1973a, fig. 35; Godefroit 1995). The triradiate form of the supratemporal can be seen in both *Stenopterygius triscissus* and *Ichthyosaurus* cf. *communis* (McGowan 1973a; Godefroit 1993b, 1994). These two species have orthogonal orientations

of the three rami that create the more transverse alignment of the posterior of the skull (see Godefroit 1994, fig. 15B and Caine & Benton 2011, fig. 3C). *Ichthyosaurus communis* also does not have the medially ascending ramus of the supratemporal towards the contact with the parietal that is present in both *Brachypterygius extremus* and *Ophthalmosaurus icenicus* (Owen 1881; McGowan 1973a). The squamosal has been identified in some specimens of *Ichthyosaurus communis*, but may be variable (Motani 1999c; Maisch & Matzke 2000b; Maisch *et al.* 2008b; Fischer 2012; Bennett *et al.* 2012). Certain neoichthyosaurian ichthyosaurs show a slight ventral emargination between the quadratojugal and jugal, such as *Ichthyosaurus communis* and possibly *Leptonectes tenuirostris* (McGowan 1973a; Maisch & Matzke 2003), whereas in *Brachypterygius extremus*, *Nannopterygius enthekiodon*, and *Ophthalmosaurus icenicus* the posteroventral margin of the quadratojugal is straight. In *Ichthyosaurus communis*, the large and offset ventral quadrate process of the quadratojugal causes this emargination as it is placed posterior to the jugal. The quadratojugal in *Ichthyosaurus communis* also does not have the long posterior groove seen in *Ophthalmosaurus icenicus* for the ventral tongue of the squamosal, and it has a well-developed facet for the postorbital on its anterior margin rather than the external covering seen in *Ophthalmosaurus icenicus*. The anterior process of the jugal in *Ichthyosaurus* tapers anteriorly between the maxilla and lachrymal along its contact with these bones (McGowan 1973a), whereas *Brachypterygius extremus* and *Ophthalmosaurus icenicus* both have broader anterior jugals.

The vomer of *Ichthyosaurus* cf. *communis* figured by McGowan (1973a, fig. 33) has a greater medial expansion in its posterior region than is seen in *Ophthalmosaurus icenicus*. The ascending bony spurs (McGowan 1973a, p. 42, fig. 22) may be equivalent to the spinous projections seen in *Ophthalmosaurus icenicus*; both support the soft tissue structures of the nasal capsule. The palatine in *Ichthyosaurus* takes much the same form as in

Ophthalmosaurus icenicus (McGowan 1973a), although poor preservation of NHMUK PV R8177 in that region makes detailed comparisons difficult. In *Ichthyosaurus*, the anterolateral process of the palatine is not as well developed as in *Ophthalmosaurus icenicus*. Dorsally, at the posterior end of the internal narial margin in *Ichthyosaurus*, is a longitudinal furrow that forms a corresponding keel ventrally, similar to *Ophthalmosaurus icenicus*. The posterior margin of the palatine of *Ichthyosaurus* is flattened, and thins at the pterygoid contact, but becomes lamellate in this region (McGowan 1973a). The epipterygoid has been identified in *Ichthyosaurus*, but infrequently. In this taxon, it takes the form of a grooved, vertical column, with a complex dorsal suture, where it meets the parietal, and is longer but narrower ventrally, where it contacts the pterygoid and was possibly joined to the quadrate via cartilage (Woodward 1886; McGowan 1973a). Sollas's (1916, p. 87, fig. 9) reconstruction of *Ichthyosaurus* aff. *communis* shows a narrower outline for the pterygoid than in *Ophthalmosaurus icenicus*. There is also a well-developed groove for the epipterygoid (*columella cranii*) that is not seen in *Ophthalmosaurus icenicus*, further supporting the lack of ossification of this element in the latter taxon. In *Ichthyosaurus*, the quadrate is slightly narrower than in *Ophthalmosaurus icenicus*. It also has a smoother-surfaced medial and dorsal margin, without so great an extent of surrounding cartilage (Sollas 1916; McGowan 1973a). Phylogenetically, the quadrate provides characters related to its dorsal articulation (Maxwell *et al.* 2012b, character 11) and position of the stapedial facet (Druckenmiller & Maxwell 2010, character 21). The stapedial facet on the quadrate is positioned on the dorsal half of the quadrate in *Ichthyosaurus* aff. *communis* (Sollas 1916; McGowan 1973a), but is more ventrally placed in *Ophthalmosaurus icenicus* and *Platypterygius australis* (see below; Wade 1990; Kear 2005).

On the opisthotic, the form and membranous structures are much the same in *Brachypterygius extremus* and *Ophthalmosaurus icenicus* as in *Ichthyosaurus*, although the

paroccipital process is more drawn out in the former species (Sollas 1916; McGowan 1973a). Lateral foramina in the supraoccipital are present in *Ichthyosaurus* as well as *Brachypterygius extremus* and *Ophthalmosaurus icenicus* (McGowan 1973a), but the former species does not have a deeply excavated supraoccipital, so only the lateral exits are present. The exoccipital of *Ichthyosaurus* has a greater extent of ossification than in *Ophthalmosaurus icenicus*, particularly in the ventral facet for the basioccipital. This facet is extended farther anteriorly in *Ichthyosaurus* and is also wider than the tongue in *Ophthalmosaurus icenicus* (Sollas 1916). McGowan (1973a) also showed a groove that cuts across the basioccipital facet on the exoccipital, possibly carrying a blood vessel. Furthermore, the anterolateral edge of the exoccipital is drawn dorsally in *Ichthyosaurus*, surrounding the vagus (jugular) foramen, and which would have contacted the otic capsule; this is formed by both the exoccipital and opisthotic in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. *Ichthyosaurus* and *Temnodontosaurus* both exhibit a large extracondylar area that may be higher or wider than the condyle itself (Seeley 1880; Owen 1881; McGowan 1973a). Additionally, *Ichthyosaurus* possesses a greatly drawn out basioccipital peg on its anterior face, only the rudiments of which can be seen in some specimens of *Ophthalmosaurus icenicus*, and of which there is no evidence at all in *Brachypterygius extremus*. The stapes in *Ichthyosaurus* is a comparatively less robust element than in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. Although also convex, the contact on the stapes with the basioccipital and opisthotic medially is not as broad in *Ichthyosaurus* as in *Ophthalmosaurus icenicus*, and may have a well-developed channel across the middle of the proximal surface of the stapes for passage of vessels (Sollas 1916; McGowan 1973a). The lateral shaft of the stapes in *Ichthyosaurus* is also bent distal to the proximal head, and the quadrate facet is narrower than in *Ophthalmosaurus icenicus*, but extended by cartilage (Owen 1881, labelled “paroccipital”).

In *Ichthyosaurus*, the splenial forms a small portion of the alveolar groove posteriorly (Home 1820; McGowan 1973a). The posterior of the splenial in *Ichthyosaurus* is also digitate, rather than tapering as seen in *Ophthalmosaurus icenicus*. The angular does not have as much exposure on the lateral face of the mandible in *Ichthyosaurus* as in either *Brachypterygius extremus* or *Ophthalmosaurus icenicus* (McGowan 1973a); the large exposure is a character of more derived ichthyosaurs (Motani 1999b, character 32; Maxwell *et al.* 2012b, character 29). The coronoid is significantly reduced in *Ichthyosaurus* (Sollas 1916; McGowan 1973a), although it is still present as a narrow splint medially in the mandible rather than lost entirely as is likely in *Ophthalmosaurus icenicus*. In *Ichthyosaurus*, the prearticular is a generally higher bone anteriorly than in *Ophthalmosaurus icenicus*. On the dorsal margin of the prearticular of *Ichthyosaurus*, there is an elongate facet for the coronoid that is not seen in *Ophthalmosaurus icenicus*, however, the posterior part does not have a well-defined coronoid peak (McGowan 1973a). Ms Joyce Townsend's illustrations of *Ichthyosaurus* cf. *latifrons* (in Romer 1968) show a low peak posterior to the coronoid process, similar to that seen in *Ophthalmosaurus icenicus*. The articular of *Ichthyosaurus* described by McGowan (1973a) has a well-developed ventral prearticular facet that is expanded downwards from the main body; this is not seen in *Brachypterygius extremus* or *Ophthalmosaurus icenicus*.

The atlas-axis in *Ichthyosaurus* is more square, particularly in posterior view, than in *Ophthalmosaurus icenicus*, and atlantal and axial intercentra may also be present in the former taxon (McGowan & Motani 2003). In *Ichthyosaurus* and some mixosaurids, the anterior cervical, and possibly more posterior, neural arches may be very tall, some reaching over twice the height of their respective vertebral centra (Owen 1881; Repossi 1902; Sander 2000; Bennett *et al.* 2012; Massare & Lomax 2014). Several taxa have fusion between the neural arches of the atlas-axis, for example, *Ichthyosaurus communis* (McGowan & Motani

2003), although it is never present in *Ophthalmosaurus icenicus*; this is a diagnostic character separating *Ophthalmosaurus icenicus* and *Ophthalmosaurus natans* (see *Discussion* below; McGowan & Motani 2003; Druckenmiller & Maxwell 2010). The gastralial basket of almost all ichthyosaurs in which it is adequately known, such as *Ichthyosaurus* and *Stenopterygius*, is constructed of three columns of gastralia: a medial element flanked by a lateral element on each side (Owen 1881; Sander 2000, character 75); it is likely that *Ophthalmosaurus icenicus* had the same arrangement.

Distal carpal two and more distal elements are notched in some specimens of *Ichthyosaurus*, with incidence of this being variable and lacking a clear taxonomic pattern (Owen 1881; McGowan 1974b; McGowan & Motani 2003). Like the elements around them, the carpals are more clearly polygonal and closely articulated in *Ichthyosaurus* than in *Ophthalmosaurus icenicus*, like in *Brachypterygius extremus*, *Caypullisaurus*, and *Platypterygius* (Broili 1907; McGowan 1974b; Fernández 2001; McGowan & Motani 2003). Unlike in *Ophthalmosaurus icenicus*, the phalanges in these taxa are not as grossly thickened dorsoventrally.

The reduced, styloid form of the ilium is found in all parvipelvian ichthyosaurs, its position and orientation being deduced from articulated specimens (Wiman 1921; Huene 1922a). More variation between taxa is found in the ischium and pubis (or ischiopubis). In more basal parvipelvian ichthyosaurs, for example *Ichthyosaurus communis*, *Ichthyosaurus breviceps*, and *Leptonectes tenuirostris*, the ilium is comparatively larger than in *Ophthalmosaurus icenicus* (Owen 1881; McGowan 1974b; Massare & Lomax 2014). In *Ichthyosaurus*, *Leptonectes*, and *Temnodontosaurus*, fusion of the ischium and pubis is variable between individual specimens, and may be present proximally, distally, or both, containing the obturator foramen (McGowan & Motani 2003). On the femur of

Ichthyosaurus, the ventral process is slightly demarcated and offset from the rest of the proximal surface (Bennett *et al.* 2012; Maxwell *et al.* 2012c; Massare & Lomax 2014).

JANUSAURUS LUNDI ROBERTS *ET AL.*, 2014

Janusaurus lundi Roberts *et al.*, 2014 from the the Sløttsmoya Member of the Agardfjellet Formation (Tithonian) is known from a single specimen that includes much of the skull and disarticulated anterior trunk region. Phylogenetic analysis places this taxon within Ophthalmosaurinae as sister to *Cryopterygius kristiansenae* and *Palvennia hoybergeti* (Roberts *et al.* 2014).

The posterior premaxilla in *Janusaurus lundi* is poorly preserved, but contacts the lachrymal extensively, unlike in *Ophthalmosaurus icenicus*, and possibly extends posteriorly to contact the anterior jugal. A similar, but smaller contact between these two bones is possible in *Brachypterygius extremus* (Text-fig. 39), but is caused by anterior extension of the jugal rather than posterior extension of the premaxilla, as in *Janusaurus lundi*. Ventrally, the maxilla of *Janusaurus lundi* has a very narrow lateral exposure, and posterior to this, the jugal has a slight ventral deflection. The prefrontal has a smaller exposure dorsally and laterally in *Janusaurus lundi* than in *Brachypterygius extremus*, and like in *Ophthalmosaurus icenicus*, approaches the external naris, but does not contact it. The postorbital region is narrow in *Janusaurus lundi*, as in *Ophthalmosaurus icenicus*, but the posteroventral quadratojugal seems to have greater lateral exposure around the ventral contact with the quadrate. While the basioccipital of *Janusaurus lundi* is crushed, the extracondylar area appears reduced in posterior view compared to *Ophthalmosaurus icenicus*, but the lateral facets for the opisthotic and stapes are more extensive than in *Palvennia hoybergeti* (see below). The stapedial shaft is gracile in *Janusaurus lundi*, not as robust as in *Ophthalmosaurus icenicus* (Pl. 11 in Part 1). The mandible of *Janusaurus lundi* has a similar

configuration to *Ophthalmosaurus icenicus*, but medially, the prearticular of *Janusaurus lundi* is more strongly developed than in *Brachypterygius extremus* or *Ophthalmosaurus icenicus*. Both the prearticular and surangular of *Janusaurus lundi* have well developed processes in the preglenoid region (paracoronoid and MAME processes), whereas in the taxa described here, these are limited to smaller processes or flanges on these bones. *Janusaurus lundi* may preserve an ossified coronoid.

The clavicles of *Janusaurus lundi* share the similar medial interdigitation articulation that Seeley (1874b) used to characterize *Ophthalmosaurus icenicus*, but in the former taxon there does not appear to be any exposure of the interclavicle between the clavicles, nor do the clavicles wrap strongly around the transverse bar of the interclavicle (Text-fig. 31 in Part 1). The ventral interclavicle of *Janusaurus lundi* has a foramen centrally and a distinct groove on the posterior bar dorsally. In *Janusaurus lundi*, the humerus follows the configuration of distal facets of *Ophthalmosaurus icenicus*, but is not so anteroposteriorly expanded distally, and the dorsal and ventral processes of the humerus are not so large, although this may be an effect of preservation. The ilium of *Janusaurus lundi* has a prominent anterodorsal process, and the ischiopubic plate end distally in a square, oblique margin; there is no obturator foramen, nor evidence of the suture between the ischium and pubis.

LENINIA STELLANS FISCHER ET AL., 2014

Leninia stellans Fischer et al., 2014 is known from a partial skull from the *Deshayesites volgensis* Ammonite Biozone (Aptian) of the Kriushi locality, Ulyanovsk Region, Russia. The phylogenetic analysis included with the original description placed *Leninia stellans* as one of the most basal ophthalmosaurines, alongside *Mollesaurus periallus* (Fischer et al. 2014; Arkhangel'sky & Zverkov 2014), whereas Roberts et al. (2014) found *Leninia stellans*

to be the sister taxon to *Ophthalmosaurus icenicus*, with these two taxa together as sister to *Acamptonectes densus* within Ophthalmosaurinae.

The prefrontal in *Leninia stellans* is excluded from contributing to the external naris by the nasal, similar to *Brachypterygius extremus*, whereas there is a small contact in *Ophthalmosaurus icenicus*. Unlike other ophthalmosaurids, the prefrontal extends anterodorsally, compressing the nasal and forming a large part of the anterodorsal skull roof. An internasal foramen is enclosed between the posteromedialmost nasals and the anteromedial frontals of *Leninia stellans*. The postfrontal contact with the supratemporal is large in *Leninia stellans* and the supratemporal has two large processes, laterally and medially, that overlap the postfrontal to a greater extent than in *Ophthalmosaurus icenicus* (Text-fig. 4 in Part 1), and does not seem to be present in *Brachypterygius extremus* (Text-figs 37, 39). The postorbital region is anteroposteriorly longer in *Leninia stellans* than in *Nannopterygius enthekiodon* and *Ophthalmosaurus icenicus*, and the postorbital and quadratojugal have a broader later exposure in the first taxon than the latter two. The extracondylar area in *Leninia stellans* is of a similar size to *Ophthalmosaurus icenicus*, and larger than in *Brachypterygius extremus*. Evidence for a stapes-supratemporal contact is seen in *Leninia stellans*, but was previously known only from *Ophthalmosaurus icenicus* and *Ophthalmosaurus natans*. Unlike in *Ophthalmosaurus icenicus* and *Janusaurus lundii* (see above; Roberts *et al.* 2014), the angular does not greatly expand dorsoventrally ventral to the orbit in *Leninia stellans*, however, the angular does become higher more posteriorly.

MAIASPONDYLUS LINDOEI MAXWELL & CALDWELL, 2006

Maiaspondylus lindoei Maxwell & Caldwell, 2006 is known from the Loon River Formation (Albian) of a locality on the Hay River, Northwest territories, Canada. The material is incomplete, but parts of the snout, basicranium, pectoral girdle and forelimb, and

vertebral column are represented by several specimens (Maxwell & Caldwell 2003, 2006). However, these are all embryos or juvenile specimens, so may show features that are subject to ontogenetic change (Johnson 1979). Phylogenetic analyses have recovered *Maiaspondylus lindoei* within Platypterygiinae, close to *Aegirosaurus leptospondylus* and *Brachypterygius extremus* (Fischer *et al.* 2012; Fischer *et al.* 2013; Roberts *et al.* 2014; Arkhangel'sky & Zverkov 2014), as sister to *Platypterygius americanus* (Druckenmiller & Maxwell 2010), or even sister to Ophthalmosauridae itself (Motani *et al.* 2015a).

The premaxilla and lachrymal in *Maiaspondylus lindoei* contact ventral to the external naris, more extensively than in *Ophthalmosaurus icenicus*, similar to *Brachypterygius extremus* (Text-fig. 39). In *Maiaspondylus lindoei*, the humerus is relatively stouter than in the taxa described above, with the proximal and distal portions having subequal widths. The distal humeral facets share their configuration with *Aegirosaurus leptospondylus* and *Brachypterygius extremus*, and the more distal forelimb elements are square.

MOLLESAURUS PERIALLUS FERNÁNDEZ, 1999

Mollesaurus periallus Fernández, 1999 is known from the Los Molles Formation (Bajocian) of Chacaico Sur, Neuquén Province, Argentina, but only from partial skull remains (Fernández 1999; Fernández & Talevi 2014). It has been recovered as one of the more basal ophthalmosaurids (Druckenmiller & Maxwell 2010), or as the most basal ophthalmosaurine ichthyosaur in phylogenetic analysis (Fischer *et al.* 2012; Fischer *et al.* 2013; Fernández & Talevi 2014; Roberts *et al.* 2014; Arkhangel'sky & Zverkov 2014).

Ventrally in *Mollesaurus periallus*, the jugal broadens anteriorly to cover much of the posterior maxilla laterally, as in *Ophthalmosaurus icenicus*. The postorbital region of *Mollesaurus periallus* is broader than in *Ophthalmosaurus icenicus*, and the squamosal is square in the former taxon rather than triangular in the latter taxon (Pl. 4, figs 1, 2 in Part 1).

However, the quadratojugal has a very narrow lateral exposure in *Mollesaurus periallus* as it is covered by the squamosal dorsally and the dorsal process of the jugal ventrally. In *Mollesaurus periallus*, the exoccipital possesses only one foramen for the passage of the XII nerve and the vagus foramen is almost entirely enclosed by the exoccipital, surrounded by the opisthotic facets. The extracondylar area of the basisphenoid of *Mollesaurus periallus* is similar to *Ophthalmosaurus icenicus*, but larger than in *Brachypterygius extremus*, and the ventral tubers and median notch are present, as in *Ophthalmosaurus icenicus*. In *Mollesaurus periallus*, the stapes has a robust lateral shaft, which is not clearly offset from the medial head as it is in *Ophthalmosaurus icenicus*. The ribs of *Mollesaurus periallus* are more robust proximally than in *Ophthalmosaurus icenicus*, with a dorsal ridge extending along the external side from the capitulum in the more anterior ribs (Talevi & Fernández 2012).

PALVENNIA HOYBERGETI DRUCKENMILLER *ET AL.*, 2012

Palvennia hoybergeti Druckenmiller *et al.*, 2012 is known from a single, moderately well-preserved skull in dorsal view from the Sløttsmoya Member of the Agardfjellet Formation (Tithonian) of Spitsbergen, Svalbard (Druckenmiller *et al.* 2012). This taxon has only been included in a phylogenetic analysis by Roberts *et al.* (2014), who found it to be within the Ophthalmosaurinae alongside *Cryptopterygius kristiansenae* and *Janusaurus lundii*.

Like *Ichthyosaurus breviceps*, the snout and premaxilla of *Palvennia hoybergeti* is relatively shorter than in the taxa described here; the premaxilla is *c.* 50% of the total skull length, but this not dissimilar to *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. Because of the short snout, the premaxillae diverge relatively far anteriorly, so that the nasals have a greater exposure dorsally than in other ichthyosaur taxa. Although poorly preserved, the external narial region suggests that the premaxilla and lachrymal of *Palvennia hoybergeti* do not contact, or if they do, that this contact is small, as in *Ophthalmosaurus icenicus* (Text-

fig. 4 in Part 1), but not as extensive as in *Brachypterygius extremus* (Text-fig. 39). Dorsally, the frontal in *Palvennia hoybergeti* have a small exposure and enclose a large pineal foramen, larger than in *Ophthalmosaurus icenicus*, that is bordered posteromedially by the parietals. The exoccipitals of *Palvennia hoybergeti*, *Platypterygius australis*, and *Ophthalmosaurus natans* make a larger contribution to the *foramen magnum* than the supraoccipital; the reverse is found in *Ophthalmosaurus icenicus* (see also the discussion of the synonymy of *Ophthalmosaurus* and *Baptanodon* below). The extracondylar area of the basioccipital in *Palvennia hoybergeti* is not visible in posterior view and there are no ventral tubers or notch, more similar to *Brachypterygius extremus* than the basioccipital of *Ophthalmosaurus icenicus*. However, the extracondylar area is extensive in lateral view and reduces the lateral articular area for the opisthotic and stapes. The stapes has a more slender shaft in *Palvennia hoybergeti* than in *Ophthalmosaurus icenicus*, although the medial head is similarly bulbous in both taxa. There is no visible suture line on the atlas-axis of *Palvennia hoybergeti*. A fragment of the humerus suggests *Palvennia hoybergeti* may have possessed a distal facet for a post-axial accessory element.

PARAOPHTHALMOSAURUS ARKHANGELSKY, 1997

As discussed above (see the generic and specific discussions of *Ophthalmosaurus* and *Ophthalmosaurus icenicus* respectively), Arkhangel'sky & Zverkov (2014) recently revised *Paraophthalmosaurus* to include *Paraophthalmosaurus saveljeviensis* and 'Yasykovia' *kabanovi*. These taxa have both been considered synonymous with *Ophthalmosaurus icenicus* (Maisch & Matzke 2000; McGowan & Motani 2003; Maisch 2010). Known remains of *Paraophthalmosaurus* include partial skeletons and pectoral material referred to *Paraophthalmosaurus saveljeviensis* (Arkhangel'sky 1997, 1998), and pectoral, forelimb, and hindlimb, material referred to *Paraophthalmosaurus kabanovi* (Efimov 1999a). All this

material derives from the middle Volgian (Tithonian) of Saratov and Ulyanovsk regions, Russia. The phylogenetic analysis of Arkhangel'sky & Zverkov (2014) recovered a monophyletic *Paraophthalmosaurus* (hence their revision of these taxa), which is within Ophthalmosaurinae and sister to the polytomy *Ophthalmosaurus icenicus*.

The prefrontal of *Paraophthalmosaurus saveljeviensis* seems to be broadly excluded from the external naris by contact between the nasal and lachrymal, similar to the condition in *Brachypterygius extremus* (Text-figs 37, 39). There is uncertainty regarding the extent of the quadratojugal and squamosal, and the presence of the latter, but in *Paraophthalmosaurus saveljeviensis*, the postorbital region is narrow, as in *Ophthalmosaurus icenicus*, with a particularly narrow postorbital bone (Text-fig. 4a in Part 1). In *Paraophthalmosaurus saveljeviensis*, the posterior lower jaw is similar in form to both *Brachypterygius extremus* and *Ophthalmosaurus icenicus*.

As in *Ophthalmosaurus icenicus*, the distal clavicles of *Paraophthalmosaurus saveljeviensis* are deflected, presumably to encompass the distal scapula. The form of the coracoids in *Paraophthalmosaurus saveljeviensis* shown by Arkhangel'sky (1997, figs 1, 2c) is unusual among ichthyosaurs: the lateral margins are straight and continuous, while the medial margins are angled obliquely and diverge posterior to the coracoidal symphysis. A similar, elongate form of the coracoid is found in *Stenopterygius*, *Paraophthalmosaurus*, and *Nannopterygius enthekiodon*, among other taxa (Text-fig. 44; Johnson 1979; Efimov 1999a; Arkhangel'sky & Zverkov 2014). However, the posterior coracoids of *Paraophthalmosaurus saveljeviensis* are angled posteromedially, while the posterior coracoids of both *Paraophthalmosaurus kabanovi* and *Nannopterygius enthekiodon* are angled obliquely posterolaterally (Efimov 1999a). This is clearly different from the more rounded posterior margin of *Ophthalmosaurus icenicus* (Text-figs 31, 32; Pl. 20, figs 5, 6, Pl. 21, figs 1–4 in Part 1), but possibly similar to the coracoid of *Brachypterygius extremus* (Text-fig. 40).

Additionally, the proximal scapula of *Paraophthalmosaurus kabanovi* is robust and has a bipartite articulation with the coracoid, enclosing the *fenestra coracoscapularis*; this feature is only otherwise seen in some specimens of *Stenopterygius* (Johnson 1979). The humerus of *Paraophthalmosaurus* has the same distal facet configuration as *Ophthalmosaurus icenicus*. The proximal humerus is wider than the distal humerus in *Paraophthalmosaurus kabanovi*, which is the case in *Nannopterygius enthekiodon* (Text-figs 43, 44) and *Macropterygius* sp. indet. approaches this (Pl. 40, figs 4–6). The femur referred by Efimov (1999a) to ‘*Yasykovia*’ *kabanovi* has three distal facets for articulation with a pre-axial accessory element, tibia, and fibula respectively, this is found in some Cretaceous taxa referred to *Platypterygius*, and *Maiaspondylus*, but is not known in the Jurassic taxa described above.

PLATYPTERYGIUS HUENE, 1922b

Platypterygius Huene, 1922b has been considered a wastebasket taxon for Cretaceous ichthyosaurs (McGowan & Motani 2003), although the material is currently being reappraised and reassigned (e.g. Fischer *et al.* 2014a, Fischer *et al.* 2014b). The genus *Platypterygius* contains nine valid species, although some of these are putative or may be composites. While many of these species have largely complete remains, the best known are *Platypterygius americanus* (Nace, 1939), *Platypterygius australis* (M’Coy, 1867), and *Platypterygius hercynicus* Kuhn, 1946, the remains of which have been re-described recently and will be the focus of the comparisons below (Romer 1968; Kear 2005; Kolb & Sander 2009; Fischer 2012; Maxwell & Kear 2010; Zammit *et al.* 2010). *Platypterygius americanus* is known from the Albian–Cenomanian of the USA with variously complete specimens that include much of the skeleton (Romer 1968; Maxwell & Kear 2010). *Platypterygius australis* is known from the Albian of Queensland, Australia, again with specimens representing much of the skeleton (Wade 1984, 1990; Kear 2005; Zammit *et al.* 2010). *Platypterygius*

hercynicus, however, is known from two specimens from the Albian of Saint-Jouin-Bruneval, Seine-Maritime, France, and the Aptian of Salzgitter, Lower Saxony, Germany (Kolb & Sander 2009; Fischer 2012). Recent phylogenetic analyses have not recovered a monophyletic *Platypterygius*, but few of the valid species have been included in any single analysis, and the genus is often paraphyletic with respect to *Caypullisaurus bonapartei* Fernández, 1997b, *Pervushovisaurus bannovkensis* Arkhangelsky, 1998, and *Simbirskiasaurus birjukovi* Otschev & Efimov, 1985 within Platypterygiinae (Fischer *et al.* 2013; Roberts *et al.* 2014).

Three-dimensionally preserved and rendered remains of *Platypterygius australis* suggest that the maxilla in this taxon was exposed along much of the posterior part of the rostrum, forming the posterior and ventral margins of the external naris and preventing the lachrymal from contributing to the external naris (Kear 2005). The dorsal extension of the maxilla in *Platypterygius australis* is interpreted as a neomorphic development, possibly of the dorsal process of the maxilla, different from the postnarial process seen in Triassic ichthyosaurs (Maisch & Matzke 2000; Kear 2005). *Platypterygius australis* also shows evidence of the tongue-like medial processes on the maxilla interpreted as support for the soft tissues of the nasal cavity, similar to those described above in *Ophthalmosaurus icenicus* (Pl. 1, figs 1, 2 in Part 1). Both *Platypterygius australis* and *Platypterygius hercynicus* show a greater development of the dorsal ridges on the nasals that surround the *excavatio internasalis* into dorsal ridges than *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, and well developed posterior processes that overlap the anterior of the postfrontal (Kear 2005; Kolb & Sander 2009; Fischer 2012). *Platypterygius australis* has a bony pillar that divides the external naris into two foramina, anteriorly and posteriorly; this is similar to the condition in *Simbirskiasaurus birjukovi* and *Pervushovisaurus bannovkensis*, although the lachrymal forms the posterior border to the external naris in that taxon (Fischer *et al.* 2014b), but clearly

differs from the undivided naris of *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. In both *Platypterygius australis* and *Platypterygius hercynicus*, the frontal has a more extensive exposure than in *Ophthalmosaurus icenicus* and contributes to the border of the supratemporal fenestra (Kear 2005; Kolb & Sander 2009; Fischer 2012). In *Platypterygius australis* there is a greater contribution by the parietals to the pineal foramen than in *Ophthalmosaurus icenicus*, whereas in *Platypterygius hercynicus*, the parietals are entirely excluded from contributing to the pineal foramen by the frontals (after Fischer 2012). The postfrontal in *Platypterygius australis* and *Platypterygius hercynicus* is a more important component of the dorsolateral skull roof than in *Ophthalmosaurus icenicus*, making up most of its margin in dorsal view (Kuhn 1946; Kear 2005; Kolb & Sander 2009; Fischer 2012). Anteriorly, the postfrontal in both *Platypterygius australis* and *Platypterygius hercynicus* is overlapped by a posterior process of the nasal and prevented from contacting the parietal (in dorsal view) by the temporal process of the frontal (Fischer 2012, fig. 2C). While a definite squamosal is not known in *Platypterygius*, Fischer (2012, p. 130) inferred its presence in *Platypterygius hercynicus* from large facets on the quadratojugal. In *Platypterygius americanus*, *Platypterygius australis*, and *Platypterygius sachicarum* Páramo, 1997 from the Paja Formation (Barremian–Aptian) of Colombia, there is no evidence of a squamosal from the surrounding bones, so its loss is considered to be real (Romer 1968; Wade 1984, 1990; Páramo 1997; Kear 2005; Fischer 2012; Kear & Zammit 2014).

The vomer of *Platypterygius australis* ascends posteriorly into a dorsal sheet, which posteriorly, has embayments similar to the extent in *Ophthalmosaurus icenicus* (Text-fig. 7; Pl. 5, 1–4 in Part 1), but dorsally, the process has a stronger tongue-and-groove suture with the nasal in *Platypterygius australis* (Kear 2005). Medially, the vomer in *Platypterygius australis* is grooved for reception of the broad anterior portion of the parasphenoid, with a larger facet dorsal to this (Kear 2005); in *Ophthalmosaurus icenicus*, this is almost entirely

held between the anterior rami of the pterygoids. In *Platypterygius australis*, the anterolateral process of the palatine forms an interdigitating suture with the maxilla, which is more complex than the tongue-and-groove structure found in *Ophthalmosaurus icenicus* (Kear 2005). Unlike in *Ophthalmosaurus icenicus*, there is no anterior extension on the palatine of *Platypterygius australis* medial to the internal naris; this medial border of the internal naris is formed entirely by the vomer in *Platypterygius australis* (Kear 2005). The pterygoid in *Platypterygius australis* has well-developed facets on the pterygoid for the epipterygoid that are not found in *Ophthalmosaurus icenicus* (Pl. 6, figs 1, 2 in Part 1), despite its apparent lack of ossification. The quadrate in *Platypterygius australis* and *Platypterygius hercynicus*, as in *Sisteronia seeleyi*, does not have a quadrate lamella dorsally as found in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, and the condylar area ventrally is more massive and angled further anteriorly than in the taxa described above (Kear 2005; Kolb & Sander 2009; Fischer *et al.* 2014a). In *Platypterygius australis*, the prootic is a hexagonal element, more angled than in *Ophthalmosaurus icenicus* (Text-fig. 11; Pl. 8, figs 1, 2 in Part 1), with a dorsally-positioned protuberance on the anterior face; whether this is due to the extent of ossification is uncertain. *Platypterygius australis* does not have the dorsal contact between the exoccipital and opisthotic found in *Ophthalmosaurus icenicus* (Kear 2005). The position of the notochord on the articular condyle is variable between *Ophthalmosaurus icenicus*, and *Platypterygius* and *Brachypterygius extremus*: in the former species, as well as in Liassic ichthyosaur taxa, the notochordal pit is placed centrally (Appleby 1961; McGowan 1973a). *Platypterygius* and *Brachypterygius extremus* clearly have more dorsally located notochordal pits (Broili 1909; Kear 2005). *Platypterygius* shows a much more expanded medial stapedial head; this was greater in *Platypterygius platydactylus* (Broili, 1907) from the Aptian of Lower Saxony, Germany, and *Platypterygius australis* than in '*Platypterygius brunsvicensis*' Broili, 1909 from the Neocomian (Berriasian–Aptian) of Lower Saxony, Germany (Wade

1990; Kear 2005). *Platypterygius hercynicus* and *Platypterygius platydactylus* also have a concave anterior margin on the stapes, rather than the straight form in *Ophthalmosaurus icenicus* (Broili 1907; Kolb & Sander 2009; Fischer 2012).

In *Platypterygius australis*, the prearticular does not extend along as much of the jaw length as in *Ophthalmosaurus icenicus* (Text-fig. 17 in Part 1), and is a higher, curved element, compared to the straighter form of the prearticular in *Ophthalmosaurus icenicus* (Kear 2005). Posteriorly, the angular forms a greater proportion of the height of the mandible in *Platypterygius australis* than in either *Brachypterygius extremus* or *Ophthalmosaurus icenicus*. *Platypterygius* and *Brachypterygius extremus* have somewhat rounder and higher articulars than in *Ophthalmosaurus icenicus* that may help identify platypterygiine ichthyosaurs (Broili 1907; Kear 2005), although shape variation seems continuous across Ophthalmosauridae. Unlike most other ichthyosaurs, tooth plication in *Platypterygius* is poorly developed and restricted more to the middle of the tooth base, which is squarer than in *Ophthalmosaurus icenicus* due to expansion by increased osteocementum (Kiprijanoff 1881; Maxwell *et al.* 2012a). *Platypterygius australis* has a thin layer of acellular cementum, which covers the enamel and orthodentine (Maxwell *et al.* 2011). The hyoids in *Platypterygius australis* and *Platypterygius hercynicus* are very similar in form to those of *Ophthalmosaurus icenicus*, but each becomes more rounded anteriorly (Kear 2005; Kolb & Sander 2009). The atlas-axis is fused to the third cervical vertebrae in *Platypterygius platydactylus* and some specimens of *Ichthyosaurus communis* (Broili 1907; Kear 2003; McGowan & Motani 2003), unlike in *Ophthalmosaurus icenicus* or any other species of *Platypterygius* or *Ichthyosaurus*.

In *Platypterygius australis*, the coracoid is small relative to the other pectoral girdle bones, and the coracoids of other ophthalmosaurids, and the anterolateral notch on the coracoid is reduced in size to a shallow embayment (Wade 1984; Zammit *et al.* 2010). The scapula of *Platypterygius americanus* and *Platypterygius australis* is greatly expanded

proximally to form a broad triangular surface that narrows greatly to the distal shaft (Maxwell & Kear 2010; Zammit *et al.* 2010). The dorsal and ventral processes on the humerus of *Platypterygius* are massive and strongly developed, larger than is found in any of the taxa described above, with the ventral process often being larger and extending distally for much of the length of the humerus. In the four taxa described above, the dorsal and ventral processes on the humerus descend into the humerus by about half of the proximodistal length of the humerus. The humerus in *Platypterygius* may have between two and four distal facets, with the ulnar facet being the largest, unlike in *Ophthalmosaurus icenicus* (Text-fig. 33 in Part 1; McGowan 1972c; McGowan & Motani 2003): *Platypterygius americanus* and *Platypterygius platydactylus* both have two distal humeral facets articulating only with the radius and ulna (Broili 1907; Nace 1939; Maxwell & Kear 2010); *Platypterygius australis* possesses three distal humeral facets, although the anterior facet is typically very small and articulates with an anterior accessory element (Wade 1984; Zammit *et al.* 2010); *Platypterygius hercynicus* has four distal humeral facets, the posteriormost articulating with the pisiform (Kuhn 1946; Kolb & Sander 2009). *Platypterygius americanus*, *Platypterygius australis*, *Platypterygius hercynicus*, and *Platypterygius platydactylus* all have two or more pre-axial accessory digits that extend the full length of the forelimb (Broili 1907; Motani 1999a; Fernández 2001; Kolb & Sander 2009; Zammit 2010; Zammit *et al.* 2010); in all these taxa, the elements take the form of the corresponding primary digital elements. While *Platypterygius hercynicus* seems to have a single post-axial accessory digit, *Platypterygius australis* has three post-axial accessory digits, and *Platypterygius platydactylus* and *Caypullisaurus bonapartei* both have two (Broili 1907; Fernández 1998, 2001; Zammit *et al.* 2010).

Like the humerus, the femur in *Platypterygius* is more massive than in *Ophthalmosaurus icenicus* (Text-figs 35, 36 in Part 1): the dorsal and ventral processes are much larger and

extend along almost the entire length of the femur (Nace 1939; Kolb & Sander 2009; Maxwell & Kear 2010; Zammit *et al.* 2010). Both of these processes are more plate-like in form and clearly offset from the main body of the femur in *Platypterygius* than in *Ophthalmosaurus icenicus*. In *Platypterygius australis*, the femur has three distal facets: the anterior facet articulates with a pre-axial accessory element (Wade 1984; Zammit *et al.* 2010; Maxwell *et al.* 2012c). This is also the case in *Platypterygius hercynicus*, but the similar size of the distal facets suggests that the femur may have articulated with the tibia, astragalus, and fibula (anterior to posterior) respectively (Kuhn 1946; Kolb & Sander 2009). The distal hindlimb elements in *Platypterygius* are, like the distal forelimb elements, rectangular, becoming rounder distally (Maxwell & Kear 2010; Zammit *et al.* 2010), which is similar to the polygonal elements in Early Jurassic taxa (McGowan 1974a, b, 1979).

SISTERONIA SEELEYI FISCHER *ET AL.*, 2014a

Sisteronia seeleyi Fischer *et al.*, 2014a is known from specimens from the Cambridge Greensand Member of the West Melbury Marly Chalk Formation (Cenomanian) and the Gault Formation (Albian) of the United Kingdom, and the Albian Vocontian Basin, France. Although the remains are incomplete, this taxon has been included in Platypterygiinae by Fischer *et al.* (2014a, p. 7).

In *Sisteronia seeleyi*, the quadrate has a well-developed stapedial facet surrounded by a bony ridge on the ventral portion of the pterygoid lamella, developed more than in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, although this feature is variable. The basisphenoid of *Sisteronia seeleyi* is massive, with elongate basiptyergoid processes that give the basisphenoid a markedly pentagonal shape in dorsal or ventral view; this may be accentuated by crushing of the holotype (Fischer *et al.* 2014a). Additionally, there is no clear groove for the facial (VII) nerve posterior to the basiptyergoid processes in *Sisteronia seeleyi*

that demarcates these processes from the main body, as there is in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. The floor of the *foramen magnum* on the basioccipital has a low dorsal process anteriorly in *Sisteronia seeleyi*, an autapomorphy of the species, and well developed opisthotic facets, which are not found in the taxa described above. As with other Platypterygiinae, the extracondylar area is greatly reduced, and the ventral portion is not visible in posterior view in *Sisteronia seeleyi*, similar to *Brachypterygius extremus* (Text-fig. 41a, b; Pl. 33, figs 5–8), but strongly reduced compared to *Ophthalmosaurus icenicus* (Text-fig. 14; Pl. 10 in Part 1). The teeth of *Sisteronia seeleyi* have strongly compressed roots, with a rectangular cross-section, rather than the square roots of *Brachypterygius extremus* and, to a lesser extent, in *Ophthalmosaurus icenicus*. Finally, the humerus of *Sisteronia seeleyi* has a small posterior distal facet for articulation with the pisiform that is not seen in the taxa described above.

STENOPTERYGIUS JAEKEL, 1904

The genus *Stenopterygius* Jaekel, 1904 is known from the Toarcian–Aalenian of Germany and the United Kingdom. Following Maisch's (2008) revision, four species are present in this genus: *Stenopterygius aaleniensis* Maxwell *et al.*, 2012b from the Aalenian of south-western Germany, *Stenopterygius quadriscissus* (Quenstedt, 1858) from the Toarcian of south-western Germany, *Stenopterygius triscissus* (Quenstedt, 1858) from the Toarcian of south-western Germany and the United Kingdom, and *Stenopterygius uniter* Huene, 1931b from the Toarcian of south-western Germany. *Stenopterygius* has most recently been recovered within Thunnosauria, and *Stenopterygius quadriscissus* defines the clade Baracromia Fischer *et al.*, 2013, which includes the taxa described above. Fernández (2007b) included *Chacaicosaurus cayi* Fernández, 1994 from the Bajocian of Neuquén Province,

Argentina, within *Stenopterygius*, but phylogenetic analyses have found *Chacaicosaurus cayi* to be separate from *Stenopterygius* (e.g. Fischer *et al.* 2013), so it is retained as separate here.

The premaxilla in *Stenopterygius quadriscissus* is similar in size to that of *Ophthalmosaurus icenicus*, with typical values of 60% of the length of the skull, but Maxwell (2012a) has shown that this value varies greatly between specimens. Contact between the lachrymal and premaxilla is apparently variable, being present in *Stenopterygius quadriscissus* but absent in *Stenopterygius triscissus* (Godefroit 1993b; Maisch & Ansgorge 2004). The premaxillae of *Stenopterygius uniter* exclude the nasals dorsally more posteriorly than in *Brachypterygius extremus* or *Ophthalmosaurus icenicus* (Huene 1931b; Maisch 2008). An unusual feature of *Stenopterygius aaleniensis* not found in the British taxa described above is a narrow contact between the postfrontal and nasal that splits the prefrontal exposure into two parts: lateral and medial, although there is evidence to suggest that this may occur in *Ichthyosaurus* (Motani 2005a; Maxwell *et al.* 2012b). The frontal in *Stenopterygius triscissus* and *Leptonectes cf. tenuirostris* is excluded from dorsal view by the posterior extension of the nasals to contact the parietals, allowing very little dorsal exposure of the frontals (Owen 1881; Godefroit 1993b; Maisch & Matzke 2003). This is greater than the coverage in *Ichthyosaurus communis* and *Ophthalmosaurus icenicus* (see above and Part 1; Motani 2005a), but similar to *Athabascasaurus bitumineus*. Like *Ichthyosaurus communis* above, the anterior postfrontal is Y-shaped from the interdigitating contacts between the anterior postfrontal and the nasal and frontal, but is rounded in *Brachypterygius extremus* and *Ophthalmosaurus icenicus* (Godefroit 1993b, 1994). A well-ossified sclerotic ring is a characteristic feature of ichthyosaurs. In skulls that have not been laterally compressed, Jurassic and Cretaceous ichthyosaurs show doming of the ring, as in '*Ichthyosaurus latifrons*' Owen, 1881 (pl. 27, fig. 1 in Part 1; = *Stenopterygius triscissus*) and *Leptonectes cf. tenuirostris* (Maisch & Matzke 2003, figs 2 & 3). In both ichthyosaurs, as well as

Ophthalmosaurus icenicus, the sclerotic ring protrudes outside (lateral to) the rim of the orbit. This may be compared to the protrusion in the chameleon, but the sclerotic ring in this taxon is much reduced and present only around the aperture itself: much of the eyeball is not surrounded. The palatine in *Stenopterygius triscissus* is also notched anteriorly on the midline where it forms the posterior portion of the internal naris. The anterior extension medial to the internal naris is reduced compared to *Ophthalmosaurus icenicus*, as is the contact with the vomer posteriorly (Seeley 1880; Owen 1881; Baur 1895; Godefroit 1993b). This is similar to the palatine of *Temnodontosaurus platyodon*, although this latter taxon has a relatively longer anterior process of the palatine than in *Stenopterygius triscissus* and *Ophthalmosaurus icenicus* (Godefroit 1993a). Compared to both *Stenopterygius triscissus* and *Temnodontosaurus platyodon*, the posterior portion of the palatine is more irregular in *Ophthalmosaurus icenicus*, as the contact with the pterygoid is an interdigitating suture in the last taxon (see Part 1). In *Stenopterygius triscissus* and *Temnodontosaurus platyodon*, the posterior contact of the palatine with the pterygoid is simpler: the pterygoid underlaps the palatine posteriorly (Seeley 1880; Owen 1881; Baur 1895; Godefroit 1993a, b; Maisch & Hungerbühler 1997). In *Stenopterygius quadriscissus* and *Stenopterygius triscissus*, the quadratojugal is larger than in *Ophthalmosaurus icenicus*, and may have extensive posterior exposure (Godefroit 1993b; Maisch & Ansgorge 2004; Caine & Benton 2011).

Although similar to that of *Ophthalmosaurus icenicus*, the interclavicle in *Stenopterygius* has a closer contact with the coracoid dorsally. The suture between the two forms a strong ridge-and-groove system (Johnson 1979). The median stem on the interclavicle is also much longer than in *Ophthalmosaurus icenicus*, extending along the entire length of the intercoracoidal suture (Caine & Benton 2011; Maxwell *et al.* 2012b). The clade Baracromia was erected by Fischer *et al.* (2013) based upon the strong development of the acromion process of the scapula found in *Stenopterygius quadriscissus* and more derived

ichthyosaurs. Many non-baracromian neoichthyosaurians have straighter dorsal and proximal margins to the scapula than the ingroup (compare *Ichthyosaurus* with *Ophthalmosaurus*).

The proximal humerus of *Stenopterygius* does not have a large and well demarcated dorsal process, unlike in the later taxa described above (Fraas 1891; McGowan & Motani 2003); however, unlike in more basal neoichthyosaurians, the ventral process is well developed, but not as large as in *Brachypterygius extremus*. As in *Nannopterygius enthekiodon*, the humerus of *Stenopterygius* has two distal facets that articulate with the radius and ulna (Huene 1931b; McGowan & Motani 2003; Maisch 2008). The distal humerus of *Stenopterygius* is expanded relative to the proximal humerus, but does not have the large anterodistal prominence of *Leptonectes* and *Temnodontosaurus* (Theodori 1854; Fraas 1891; Maisch 2008). The intermedium in *Stenopterygius* is straight distally, but may appear pointed due to the variable size of the unequal distal intermedial facets (McGowan 1979; Maisch 2008; Maxwell *et al.* 2012b); distally, the intermedium is pointed in both *Brachypterygius extremus* and *Ophthalmosaurus icenicus*, but is rounded in *Nannopterygius enthekiodon*. Post-axial accessory elements are present in many neoichthyosaurians, and they are well-known in *Ichthyosaurus*, *Stenopterygius*, and *Temnodontosaurus* (Huene 1922b; McGowan 1974a, b, 1979; Motani 1999a; Maisch 2008). Many of these elements are distal ossifications that cannot be considered digits as they are not supported proximally in the metacarpal row, and so do not extend for any great length of the forelimb (Maxwell 2012b). Their occurrence may be a result of ossification of these elements or variable preservation potential.

In *Stenopterygius* and more derived ichthyosaurs, the ilium has essentially the same form as that found in *Ophthalmosaurus icenicus* (Huene 1952). Fusion of the ischium and pubis is found only in Neoichthyosauria, but only to a similar extent as found in *Ophthalmosaurus icenicus* within the clade Baracromia (Fischer *et al.* 2013). The form of the ischiopubis is similar between *Ophthalmosaurus icenicus* and *Stenopterygius*, although the

latter possesses a generally straighter distal margin (Wiman 1921; McGowan & Motani 2003). An anterior tibial notch is also found in the Lower Jurassic taxa *Suevoleviathan* and *Stenopterygius* spp., among others (McGowan 1979; Maisch 1998a; Caine & Benton 2011; Fischer *et al.* 2011a; Maxwell 2012b). Many Lower Jurassic taxa also have anterior notching on more distal phalangeal elements, such as *Temnodontosaurus*, *Stenopterygius*, and *Suevoleviathan* (McGowan 1974a; Caine & Benton 2011; Fischer *et al.* 2011a; Martin *et al.* 2012). Notching in these taxa, and particularly in the numerous specimens of *Ichthyosaurus* is highly variable in extent (McGowan 1974b; Bennett *et al.* 2012; Maxwell *et al.* 2014).

SVELTONECTES INSOLITUS FISCHER *ET AL.*, 2011

Sveltonectes insolitus Fischer *et al.* (2011) from the Barremian of the Ulyanovsk Region, Russia, is known from a single, nearly complete specimen. In phylogenetic analyses, *Sveltonectes insolitus* is typically recovered within Platypterygiinae as sister taxon to *Aegirosaurus leptospondylus* (Fischer *et al.* 2011; Fischer *et al.* 2012; Fischer *et al.* 2013; Roberts *et al.* 2014; Arkhangelsky & Zverkov 2014), but was positioned within Ophthalmosauridae, close to both *Brachypterygius extremus* and *Ophthalmosaurus icenicus* in the analysis of Motani *et al.* (2015a).

Similar to *Acamptonectes densus* above, in *Sveltonectes insolitus*, the maxilla is covered extensively by the surrounding elements, so it is only exposed in a narrow portion ventrally on the snout. The contact between the premaxilla and lachrymal is more extensive than in *Brachypterygius extremus*, and the corresponding exposure of the maxilla is less in *Sveltonectes insolitus* than in the former species. Unusually among ichthyosaurs, the external naris of *Sveltonectes insolitus* has an elongate, hook-like descending process on the ventral border of the naris, which is comparable to the external narial pillars found in *Platypterygius australis* and *Simbirskiasaurus birjukovi* (Kear 2005; Fischer *et al.* 2011; Fischer *et al.*

2014b). Unlike in *Ichthyosaurus communis*, the internasal foramen in *Sveltonectes insolitus* is relatively tiny, placed further posteriorly, and is posteriorly enclosed by the frontals. Dorsally on the skull, the frontal of *Sveltonectes insolitus* forms part of the margin to the supratemporal fenestra, separating the parietal and postfrontal contributions; this is not the case in *Ophthalmosaurus icenicus* (Text-fig. 4 in Part 1), however, the preservation of specimens of *Brachypterygius extremus* makes the condition in that taxon uncertain. The posterior end of the pterygoid of *Sveltonectes insolitus* is developed into two prominent processes that are not found in either *Brachypterygius extremus* or *Ophthalmosaurus icenicus*. The basisphenoid of *Sveltonectes insolitus* is trapezoidal, with reduced basioccipital processes, smaller than in both *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. The dorsal surface of the basisphenoid in *Sveltonectes insolitus* is extended posterolaterally on each side to create a “kidney-shaped” surface (Fischer *et al.* 2011, p. 1013), which differs from the square dorsal surface of *Brachypterygius extremus* and the rounded dorsal surface in *Ophthalmosaurus icenicus*. The prootic of *Sveltonectes insolitus* is pierced anteriorly by a foramen just ventral to the midpoint that is not present in the taxa described here. The exoccipital of *Sveltonectes insolitus* is unusual among ophthalmosaurids (Fischer *et al.* 2011): the anterior process is reduced compared to other ophthalmosaurid taxa; there is a single large foramen in the base, as in *Mollesaurus periallus* (Fernández 1999; Fernández & Talevi 2014); and there is a groove dorsally that separates the supraoccipital facet from a pillar-like process posteriorly. As in other Platypterygiinae, the extracondylar area of the basioccipital is reduced: in *Sveltonectes insolitus*, the extracondylar area is similar in extent to *Brachypterygius extremus*. However, the basioccipital of *Sveltonectes insolitus* differs from *Brachypterygius extremus* in having a smaller anterior articular surface with a rounded anteroventral fossa ventral to this articulation. Unlike in *Ophthalmosaurus icenicus*, *Sveltonectes insolitus* does not have a *fossa surangularis* on the surangular, and the angular

has less lateral exposure than in *Ophthalmosaurus icenicus*, more similar to *Brachypterygius extremus*.

The distal ends of the transverse bar of the interclavicle in *Sveltonectes insolitus* have posterodorsal extensions, rather than the straight transverse form of *Ophthalmosaurus icenicus*. The coracoid of *Sveltonectes insolitus* is triangular laterally where the scapular facet is strongly angled anteriorly and separated from the glenoid facet; this is similar to *Nannopterygius enthekiodon* and possibly to *Brachypterygius extremus*. Additionally, the acromion process on the scapula of *Sveltonectes insolitus* is large, narrow, and clearly separated from the coracoid facet and the main body of the scapula; the acromion process of *Ophthalmosaurus icenicus* is only demarcated from the body of the scapula by its size, whereas in *Brachypterygius extremus* the acromion process is continuous with the dorsal margin of the scapula. The humerus of *Sveltonectes insolitus* has only two distal facets – as in *Nannopterygius enthekiodon* and *Macropterygius* described above – that are equal in size, which differs from both of the latter two taxa. Nonetheless, *Sveltonectes insolitus* possesses one each of a complete pre-axial and post-axial accessory digit, like in both *Brachypterygius extremus* and *Ophthalmosaurus icenicus*; the post-axial accessory digit is better developed in *Sveltonectes insolitus* than in *Ophthalmosaurus icenicus*. The distal manual elements of *Sveltonectes insolitus* are mostly polygonal except for the most distal elements, of which there are more than in either *Brachypterygius extremus* or *Ophthalmosaurus icenicus*.

The obturator foramen is lost entirely in the ischiopubis of *Sveltonectes insolitus*. The femur of *Sveltonectes insolitus* has well developed dorsal and ventral processes, and in particular, the dorsal process is more robust than found in the femur of *Ophthalmosaurus icenicus*. Both *Sveltonectes insolitus* and *Platypterygius australis* have a pedal pre-axial accessory element; *Sveltonectes insolitus* also has a post-axial accessory element, totalling five digits in the hindlimb, neither of which are present in *Ophthalmosaurus icenicus*. While

Ophthalmosaurus icenicus shows a trend to reduction of the size of the hindlimb elements and musculature; in *Sveltonectes insolitus* and *Platypterygius australis*, this was perhaps not so strong, when compared to body size, and the total number of hindlimb elements. The hindlimb of *Sveltonectes insolitus* possesses five digits, each with up to 12 elements, many more than are known for *Ophthalmosaurus icenicus*.

TEMNODONTOSAURUS LYDEKKER, 1889

Temnodontosaurus Lydekker, 1889 is a genus of basal neoichthyosaurian from the Early Jurassic. Five species are present in this genus: *Temnodontosaurus azerguensis* Martin *et al.*, 2012, *Temnodontosaurus eurycephalus* McGowan, 1974a, *Temnodontosaurus nuertingensis* (Huene, 1931a), *Temnodontosaurus platyodon* (Conybeare, 1822), and *Temnodontosaurus trigonodon* (Theodori, 1843).

The supranarial process of the premaxilla in *Temnodontosaurus platyodon* extends farther along the dorsal border of the external naris than in *Ophthalmosaurus icenicus* and *Brachypterygius extremus* (McGowan 1974a; McGowan & Motani 2003). In *Temnodontosaurus platyodon* and *Temnodontosaurus trigonodon*, the supratemporal develops a dorsolateral flange that overlaps the squamosal externally (Maisch 1997c; Maisch & Hungerbühler 2001). There are differences in the number of sclerotic plates present in the orbit, for example, *Temnodontosaurus platyodon* has 13 plates compared to the 15 in *Ophthalmosaurus icenicus* and 14 in *Brachypterygius extremus* (Home 1814, pl. 17; Owen 1881, pl. 31, fig. 2; McGowan & Motani 2003, pl. 5). In *Temnodontosaurus trigonodon*, the quadratojugal forms a straight, but more horizontal, ventral margin in which the dorsal process of the jugal is weakly developed (Maisch & Hungerbühler 2001); the ventral quadratojugal is covered by the posterior dorsal process of the jugal in *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. Maxwell *et al.* (2012b), in their data matrix, code

Temnodontosaurus platyodon and *Temnodontosaurus trigonodon* as having a poorly developed dorsal ramus of the jugal, unlike most other neoichthyosaurians (McGowan 1974a; Maisch & Hungerbühler 2001). More basal neoichthyosaurians, such as *Temnodontosaurus platyodon*, have a shorter and more robust paroccipital process, directed laterally, than in ophthalmosaurids (Godefroit 1993a). The exoccipital and stapedial facets on the opisthotic of *Temnodontosaurus platyodon* proximally face more medially than in *Ophthalmosaurus icenicus*, in which the stapedial facet faces ventrally. *Temnodontosaurus* cf. *trigonodon* has a dorsoventrally high supraoccipital that contributes little to the *foramen magnum*, and is pierced by several foramina through the posterior face of the arch (Maisch 2002, although this is a juvenile specimen). *Temnodontosaurus trigonodon*, *Temnodontosaurus platyodon*, and *Ichthyosaurus communis* all have divergent anterior processes on the supraoccipital, matched by the dorsal facet on the exoccipital (McGowan 1973a, 1974a; Godefroit 1993a; Maisch 2002), whereas in *Brachypterygius extremus* and *Ophthalmosaurus icenicus* the anterior processes of the supraoccipital are parallel. Unlike in Thunnosauria, more basal neoichthyosaurians, for example *Temnodontosaurus* and *Suevoleviathan*, do not have clearly separated rib heads, despite having two articulations proximally with the vertebrae (Huene 1922b; McGowan 1979; Maisch 1998a, b; Maisch & Matzke 2000, character 53). The clavicles in *Ichthyosaurus* and *Temnodontosaurus* are not as strongly deflected dorsally as in *Ophthalmosaurus icenicus*, and their posterior architecture is more generally concave (Owen 1881; McGowan 1974a, b, 1994b); this is due largely to the lack of a prominent acromion process of the anteroproximal scapula. In *Temnodontosaurus*, the obturator foramen is broader than in *Ophthalmosaurus icenicus*, resulting in the anterior margin of the ischium being emarginated (Owen 1881).

UNDOROSAURUS EFIMOV, 1999b

The original description of *Undorosaurus* Efimov, 1999b presented several species, but these have typically been synonymized with the type species, *Undorosaurus gorodischensis* Efimov, 1999b, since (e.g. McGowan & Motani 2003; Maisch 2010). Available material is limited to teeth, vertebral, pectoral, forelimb, pelvic, and hindlimb elements from the middle Volgian (Tithonian) of Ulyanovsk Region, Russia. Recently, *Undorosaurus gorodischensis* has been included in phylogenetic analyses, which find it to be either a basal ophthalmosaurid (Roberts *et al.* 2014), or a derived ophthalmosaurine in a polytomy with *Acamptonectes densus*, *Cryopterygius kristiansenae*, *Ophthalmosaurus icenicus*, *Ophthalmosaurus natans*, and *Paraophthalmosaurus* (Arkhangelsky & Zverkov 2014). *Undorosaurus trautscholdi* Arkhangelsky & Zverkov, 2014 was described from an incomplete forelimb from the upper Volgian (Tithonian–Berriasian) of Moscow, Russia.

The coracoids of *Undorosaurus gorodischensis* have well developed anterior medial processes, similar to *Ophthalmosaurus icenicus*, however, the scapular facet of the coracoid is not so large as in the latter taxon. Posteriorly, the margin of the coracoid is rounded and not angled obliquely as in *Nannopterygius enthekiodon*. In the specimens referred to *Undorosaurus* by Efimov (1999b), the scapula has a similar variability to *Ophthalmosaurus icenicus*, particularly in the variable development of the acromion process proximally. The humeri of both *Undorosaurus gorodischensis* and *Undorosaurus trautscholdi* are robust like *Ophthalmosaurus icenicus*, but not so anteroposteriorly elongate distally as in both *Brachypterygius extremus* and *Ophthalmosaurus icenicus*. In *Undorosaurus trautscholdi*, there are four distal humeral facets: an additional posterior facet articulates with the pisiform, which is located posterior to the ulna. This condition is similar to *Brachypterygius extremus*, although the pisiform is not so well developed in this taxon, and *Undorosaurus trautscholdi* has an additional post-axial accessory element that articulates with the posterodistal ulna, as

does the pisiform of *Ophthalmosaurus icenicus* in the interpretation in Part 1 (Text-fig. 33g). In *Undorosaurus gorodischensis*, the pisiform has a broad contact with the posterodistal ulna, larger than in both *Ophthalmosaurus icenicus* and *Undorosaurus trautscholdi* (Arkhangelsky & Zverkov 2014). The forelimb epipodials of *Undorosaurus trautscholdi* are more angular and in closer contact than in *Ophthalmosaurus icenicus*, with well defined facets between them; more distal elements become rounded and more separate. The ischiopubis of *Undorosaurus gorodischensis* differs markedly from *Ophthalmosaurus icenicus* in its lack of distal fusion between the two bones, enclosing the obturator ‘foramen’ only proximally.

DISCUSSION

OPHTHALMOSAURUS ICENICUS IN THE KIMMERIDGE CLAY?

To date, there is no conclusive evidence for the presence of *Ophthalmosaurus* in the Kimmeridge Clay Formation of Britain. Records of this taxon have mostly been founded on humeral material, which, due to the number of more recently identified ophthalmosaurid taxa, is now non-diagnostic at this level (see the taxonomic discussion in Part 1 and *Taxa invalida* above; Fischer *et al.* 2011). Cope (1967, p. 10) claimed to have found the anterior part of a skeleton of *Ophthalmosaurus*, and further remains have been found at Westbury (Grange *et al.* 1996). Assignment of the material is not helped by its generally incomplete and often fragmentary nature.

Perhaps the most likely example of *Ophthalmosaurus* is NHMUK PV 41237, from the Kimmeridge Clay Formation of Weymouth, which includes several skull elements that are consistent with the diagnosis for *Ophthalmosaurus icenicus* in Part 1; this does, however, represent a juvenile. Several basioccipitals provide strong indication that *Ophthalmosaurus* is present as they possess the following combination of characters unique to this taxon: (1)

partly reduced extracondylar area (ophthalmosaurine synapomorphy, excluding Platypterygiinae; Fischer *et al.* 2014, p. 66); (2) articular condyle clearly offset from extracondylar area (excludes *Mollesaurus periallus*; Fernández & Talevi 2014, p. 51); (3) no deep anterior fossa (excludes *Mollesaurus periallus*; Fernández & Talevi 2014, p. 51); (4) left and right extracondylar areas separated by a ridge ventrally (excludes *Acamptonectes densus* and *Leninia stellans*; Fischer *et al.* 2012, pp. 12–13; Fischer *et al.* 2014, p. 66). These characters are found in OUMNH J12450 and J12451, among others. Separation of *Ophthalmosaurus icenicus* from *Ophthalmosaurus natans* based on this element is not possible. However, the description of Gilmore (1905) suggests that the ventral portion of the extracondylar area may be larger in *Ophthalmosaurus icenicus* than in *Ophthalmosaurus natans*. The morphology of the basioccipitals in *Cryptopterygius kristiansenae* and *Nannopterygius enthekiodon* is currently unknown beyond being of the “typical ophthalmosaurid condition” (see above; Druckenmiller *et al.* 2012, p. 317).

Attempting to characterize and separate humeri is difficult, although *Cryptopterygius kristiansenae* and *Nannopterygius enthekiodon* can be excluded immediately (see above; Druckenmiller *et al.* 2012). Humeral morphology of Ophthalmosaurinae is generally similar, but separate from Platypterygiinae (Fischer *et al.* 2011). Fischer *et al.* (2012, table 2) attempted to separate *Acamptonectes densus* using the ratio “length of AAE [anterior accessory element] facet/length of radial facet”, but their values (c. 27%–32%), while generally lower, fall in the range for humeri referable to *Ophthalmosaurus icenicus* (Table 4 in Part 1). The humeri of *Mollesaurus periallus* and *Leninia stellans* are unknown (Fernández & Talevi 2014; Fischer *et al.* 2014). The form of the humerus in *Arthropterygius chrisorum* is also different enough to exclude this taxon: the dorsal and ventral processes are reduced compared to *Ophthalmosaurus* (Maxwell 2010). Following these comparisons, it is likely that at least some of the humeri represent *Ophthalmosaurus*, but again, it is not possible to

distinguish whether these are *Ophthalmosaurus icenicus* or *Ophthalmosaurus natans* (see below). In conclusion, it is highly probable that *Ophthalmosaurus*, or a very similar form, was present in the Kimmeridge Clay Formation of Britain, but identification to species level is not possible with the incomplete and fragmentary material available.

SYNONYMY OF *OPHTHALMOSAURUS* AND *BAPTANODON*

The first ichthyosaur remains from the Middle or Upper Jurassic of the USA were described by Marsh (1879) from the ‘*Sauranodon* Beds’ (later ‘*Baptanodon* Beds’) of Wyoming, and named *Sauranodon natans* Marsh, 1879. This material included several skulls and later a limb separated as *Sauranodon discus* Marsh, 1880a. Recent work has placed the source of many of these and more recently found specimens as the Redwater Shale Member, Sundance Formation of Wyoming (Massare *et al.* 2006), which has an Upper Jurassic age (Lower–Middle Oxfordian: Imlay 1982; Kvale *et al.* 2001; Massare *et al.* 2014). Marsh (1880a) erroneously identified the limb he described as a hindlimb, although its form is essentially identical to the *Ophthalmosaurus icenicus* forelimb described by Seeley (1874b). Gilmore (1905) corrected the identification of this material as the forelimb. Marsh (1880b), later realizing the genus *Sauranodon* was preoccupied, amended this to *Baptanodon* Marsh, 1880b. Baur (1887a) and Lydekker (1888) considered the remains of *Baptanodon* to be similar enough to *Ophthalmosaurus* to be synonymous. Lydekker (1889) later considered the absence of teeth in specimens of *Baptanodon* to be enough to separate *Baptanodon* and *Ophthalmosaurus* once more. New specimens of *Baptanodon* from Wyoming described by Gilmore (1902) had teeth associated with them and placed *in situ*. Gilmore suggested that *Baptanodon* and *Ophthalmosaurus* might be congeneric, but was uncertain that the specimen was truly referable to *Baptanodon* and so erected *Microdontosaurus petersonii* Gilmore, 1902 in the interim. Gilmore (1903) later described teeth and alveolar grooves in the type

specimens of *Baptanodon* following additional preparation, an important discovery that had to be repeated later by Holland (1908), as several authors had missed Gilmore's notice. He thus abandoned *Microdontosaurus petersonii*, but refrained from formally synonymizing *Ophthalmosaurus* and *Baptanodon* pending discovery of distinguishing characters. In his comparison of *Baptanodon* and *Ophthalmosaurus*, Knight (1903) named the species *Baptanodon marshi* Knight, 1903 and identified the following characters in *Baptanodon*: (1) reduced or absent interclavicle, (2) no intercentrum between vertebrae two and three, (3) large medial facets on the coracoids (intercoracoidal facets) and (4) more robust limbs. None of these are unique to *Baptanodon*, character (1) is not valid, neither do they adequately separate that genus from *Ophthalmosaurus*.

Gilmore (1905, 1906) made the first complete description and taxonomic review of *Baptanodon* (Text-fig. 45). He identified (p. 126) three characters in *Baptanodon* to separate the two genera: (1) clavicles meet medially without suture, (2) amphicoelous anterior cervical vertebrae and (3) a sixth digit, dismissing the features that Knight had previously identified (pp. 118–120). Again, these characters do not justify a generic separation between *Baptanodon* and *Ophthalmosaurus*: only the first character is a valid difference. He also erected *Baptanodon robustus* Gilmore, 1906. A further specimen described by Gilmore (1907) and named as *Baptanodon reedi* Gilmore, 1907 brought the number of species within *Baptanodon* to five: *Baptanodon natans*, *Baptanodon discus*, *Baptanodon marshi*, *Baptanodon robustus*, and *Baptanodon reedi*.

Andrews (1907), in preparation of his catalogue of the Leeds Collection of marine reptiles, noticed the large amount of variation present between specimens referred to *Ophthalmosaurus icenicus* and the ensuing errors in description and reconstruction. Here, and later (Andrews 1910), he considered the overlap in form between *Baptanodon* and *Ophthalmosaurus*, and the lack of distinguishing characters, to preclude separation of the two

genera. Williston (1914) admitted the similarity but listed figures as “*Baptanodon* (*Ophthalmosaurus*)” (e.g. captions to figs 54, 55). The congeneric status was accepted by Huene (1922b), but he listed only two of the above five species of *Baptanodon* as valid: *Ophthalmosaurus natans* and *Ophthalmosaurus discus*, as did Kuhn (1934).

The issue was revisited by Appleby (1956) as he re-described the occipital and otic regions of the skull of British *Ophthalmosaurus* material. Appleby identified several new characters of the skull that he posited could more reliably separate *Baptanodon* and *Ophthalmosaurus* (Table 11). These characters, Appleby claimed, are important as they are discrete states, not the extremes of continuous variation. As they refer to the structure of the occipital region and jaw articulation, he thus considered them significant at the generic, rather than specific level. Kirton’s (1983, p. 12) review found the two genera congeneric, dismissing all of Appleby’s characters as the result of inaccurate reconstructions (see below). This view was upheld by later authors (e.g. Maisch & Matzke 2000; McGowan & Motani 2003). Most recently, phylogenetic analyses have found *Ophthalmosaurus* (as represented by *Ophthalmosaurus icenicus* and *Ophthalmosaurus natans*) to be paraphyletic with respect to other taxa. The analyses of Druckenmiller & Maxwell (2010) and Fischer *et al.* (2013) included 10 characters with different codings between the two taxa (Table 12). Other similar analyses have shown these Ophthalmosauridae ingroup-clades to be unstable, prone to wander and to often collapse in strict consensus (e.g. Druckenmiller & Maxwell 2014; Fischer *et al.* 2014).

The first three of Appleby’s (1956) characters are the result of variation in the ossification of the supratemporal, which may vary greatly in shape (see above). Gilmore (1905, pl. 11) showed that his specimen (CMNH 878; Text-fig. 45) has been obliquely compressed, which may have affected the position and extent of the parietal. In comparison with Appleby’s (1956, fig. 2B) reconstruction, the reconstruction presented in Text-fig. 16 in

Part 1 reduces the disparity between the two taxa in this region. Appleby's (1956) last three characters are again resolved by amending the reconstruction. In particular, he did not correctly articulate the distal end of the opisthotic with the true facet on the supratemporal, instead locating it at the apex between the medial and ventral rami (Appleby 1956, p. 413). This results in the lowering and widening of the skull generally and the spreading of the posterior fenestrae in the occipital–otic region. The relative composition of the *foramen magnum* (supraoccipital or exoccipital dominated) appears to be a valid character (Maxwell *et al.* 2012b).

Phylogenetic analyses have added a few characters (Table 12) that shall be discussed. Character 1: in *Ophthalmosaurus icenicus*, the contact between the premaxilla and lachrymal is a small overlap, whereas in *Ophthalmosaurus natans*, these two bones are narrowly separated. Character 2: the anterior ramus of the jugal is broader in many ophthalmosaurids but varies within other taxa, as in *Stenopterygius* and *Temnodontosaurus*. Character 3: as with character 1, the contact between the prefrontal and external naris is small in *Ophthalmosaurus icenicus*. Character 4: the frontals do not have an extensive participation in the supratemporal fenestra in *Ophthalmosaurus icenicus* (see description and Text-fig. 4b in Part 1). Character 5: the state in *Ophthalmosaurus natans* is more variable than in *Ophthalmosaurus icenicus*, therefore there is overlap between these two taxa. The above characters are minor differences between these two taxa that may separate *Ophthalmosaurus icenicus* and *Ophthalmosaurus natans* in a phylogenetic analysis due to the definitions of the characters and states. Characters 6–9: these are valid characters to separate the two taxa. Character 10: the deltopectoral crest (ventral process) appears to be as large and well developed in *Ophthalmosaurus natans* as in *Ophthalmosaurus icenicus*, although it may be directed more anteriorly in the former reducing its apparent size (Knight 1903; Gilmore 1905). These characters, as is the recent consensus, best represent differences at the species

level and do not provide support for the separation of the genera *Ophthalmosaurus* and *Baptanodon*. Further study of material referred to *Ophthalmosaurus natans*, and more character- and taxonomically-inclusive phylogenetic analyses will be integral to fully resolving this.

PALAEOBIOGEOGRAPHY OF MIDDLE AND LATE JURASSIC ICHTHYOSAURS

In the Middle and Late Jurassic, ichthyosaurs had a wide distribution. Occurrences have been recorded on almost every continent and continuously between the high northern and southern latitudes (Text-fig. 46). The relative abundance of material from Europe and the USA is dominated by historical collections. However, more recent finds have greatly extended this range to Spitsbergen, Norway; Russia; Mexico, and Argentina (McGowan & Motani 2003; Gasparini & Fernández 2005; Druckenmiller *et al.* 2012; Frey & Stinnesbeck 2014).

While ichthyosaur diversity was thought to be lower in the Middle and Late Jurassic than in the Early Jurassic (Fernández 1997a), recent finds and taxonomic revision have increased this somewhat. The earliest diagnostic ichthyosaur remains from the Middle–Upper Jurassic series are known from the Aalenian of south-western Germany (Text-fig. 46a), representing the baracromian ichthyosaur *Stenopterygius aaleniensis* (Maxwell *et al.* 2012b). Further Aalenian–Bajocian remains are known from Patagonia, Argentina, including *Chacaicosaurus cayi*, sister taxon to Ophthalmosauridae (*sensu* Fischer *et al.* 2011), and *Mollesaurus periallus* (Fernández & Talevi 2014). More basal, non-ophthalmosaurid ichthyosaurs gradually reduced in diversity through the Toarcian–Bajocian, however, the basal thunnosaurian *Malawania anachronus* is known from the Early Cretaceous (Fischer *et al.* 2013). The most basal ophthalmosaurid, *Arthropterygius chrisorum*, is, however, only certainly known from the Oxfordian–Kimmeridgian of Melville Island, Canada, then at the

edge of the Boreal Ocean, suggesting a ghost range from the Aalenian–Oxfordian (Russell 1993; Maxwell 2010; Fischer *et al.* 2013). Additional material is referred to this genus from the Late Jurassic of Argentina (Text-fig. 46b; Fernández & Maxwell 2012). These data suggest that Ophthalmosauridae originated in the south-eastern part of the Pacific Ocean in the Aalenian–earliest Bajocian (Fernández 2003), with occurrences of ophthalmosaurids in the Tethys Ocean by the Bathonian (Delair 1985). An ophthalmosaurine ophthalmosaurid ichthyosaur from the Early Bajocian of Alaska indicates that both divergence of the two ophthalmosaurid subclades (Ophthalmosaurinae and Platypterygiinae) and widespread dispersal occurred rapidly (Druckenmiller & Maxwell 2014). This rapid dispersal is not surprising considering the morphological and physiological adaptations of thunniform ichthyosaurs to long distance, open ocean travel (Bernard *et al.* 2010; Bardet *et al.* 2014).

In the Callovian–Tithonian (Portlandian), most ichthyosaur diversity, along with most specimens, is concentrated in the peri-Tethyan region. Finds of *Ophthalmosaurus* – *Ophthalmosaurus icenicus* between western Europe and Mexico (Buchy 2010), *Ophthalmosaurus natans* in the USA, and *Ophthalmosaurus yasykovi* – support interchange along much of the western portion of the Tethys Ocean and through the ‘Hispanic Corridor’ into the Pacific Ocean (Bardet *et al.* 2014). Specimens referred to *Brachypterygius* are known from the eastern part of the Tethys Ocean, the Boreal Ocean, and Mexico (Arkhangelsky 2000; Buchy & López-Oliva 2009; Angst *et al.* 2010), with likely transfer along the ‘Viking Corridor’ (Bardet *et al.* 2014). However, the preservation and incomplete nature of SESNE 2010.0.1 casts doubt on its referral to *Brachypterygius* sp.: no diagnostic features are found in this specimen (see *Diagnosis* for *Brachypterygius extremus* above). Europe, at this time, was positioned at the confluence of the southern end of the ‘Viking Corridor’ with the western Tethys Ocean (Text-fig. 46b): this exchange and the relatively shallow, productive seas here may explain the comparatively high numbers of marine reptiles present. Finds of ichthyosaur

material in the Late Jurassic of Madagascar and South America show that, by the Tithonian, there existed a clear transfer route through the ‘Mozambique Channel’ (Bardet *et al.* 2014). Possible finds of *Brachypterygius* suggest this wide-ranging taxon had extended its range to Gondwana (Fernández 1997a), but these materials also are non-diagnostic (see discussion of *Brachypterygius* above). Jurassic ichthyosaurs from eastern Gondwana are almost unknown: despite there being a comparatively good Cretaceous record, little of this represents appropriate facies for ichthyosaur remains (Zammit 2010, 2011). Material from Antarctica is rare and often too poorly preserved to be certain of the presence of ichthyosaurs (Whitham & Doyle 1989; Hikuroa 2009). The recent finds of Upper Jurassic–Lower Cretaceous ichthyosaurs from Spitsbergen show a clear ability to survive cold-water palaeoenvironments (Druckenmiller *et al.* 2012). These, and other specimens from palaeolatitudes north of 60°N and south of 60°S (Whitham & Doyle 1989; Zammit 2011), support previous hypotheses on the thermoregulatory capabilities of marine reptiles (Bernard *et al.* 2010). Despite the presence of the ‘Viking Corridor’ between Spitsbergen and the United Kingdom, there is no species overlap between these two localities (Angst *et al.* 2010; Druckenmiller *et al.* 2012). Into the Cretaceous, the diversity of ichthyosaurs remains similar to the Late Jurassic. Taxonomic reappraisal is altering this hypothesis, but ichthyosaurs retain their worldwide distribution (McGowan & Motani 2003; Fischer *et al.* 2014a).

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Mupe Member

Muschelkalk

mutabilis, *Aulacostephanus*; Text-fig. 3

[*Myobradypterygius*]

Nannopterygius; Text-figs 43, 44, 46; Pl. 39, figs 1–5

[*Nannopterygius entheciodon*]

[*Nannopterygius entheckiodon*]

Nannopterygius enthekiodon; Text-figs 43, 44, 46; Pl. 39, figs 1–5

[*Nannopterygius euthecodon*]

natans, *Ophthalmosaurus*; Text-figs 45, 46

[*natans*, *Sauranodon*]

Neocomian

Neoichthyosauria

neoscapularis, *Callawayia*

neubigi, *Phantomosaurus*

Neuquén Province

Nevada

nichollsi, *Cymbospondylus*

Norfolk

[*normanniae*, *Ichthyosaurus*]

Northwest Territories

Norway

nuertingensis, *Temnodontosaurus*

[*Ophtalmosaurus*]

[*Ophthalmosaurus icenicus*]

Ophthalmosauria

Ophthalmosauridae

Ophthalmosaurinae

Ophthalmosaurus; Text-figs 1, 4–36, 45, 46; Pls 1–30

[*Ophthalmosaurus chrisorum*]

[*Ophthalmosaurus cuvieri*]

[*Ophthalmosaurus dilatatus*]

[*Ophthalmosaurus discus*]

Ophthalmosaurus icenicus; Text-figs 1, 4–36, 46; Pls 1–30

[*Ophthalmosaurus monocharactus*]

[*Ophthalmosaurus monocharactus*]

Ophthalmosaurus natans; Text-figs 45, 46

[*Ophthalmosaurus pleydelli*]

[*Ophthalmosaurus saveljeviensis*]

[*Ophthalmosaurus thyreospondilus*]

[*Ophthalmosaurus thyreospondylus*]

‘*Ophthalmosaurus undorensis*’

Ophthalmosaurus yasykovi; Text-fig. 46

[*Otschevia*]

[*Otschevia pseudoscythica*]

[*Otschevia zhuravlevi*]

[*ovalis*, *Ichthyosaurus*]

[*ovalis*, *Macropterygius*]

Oxford; Text-fig. 2

Oxford Clay Formation; Text-fig. 3

Oxfordian

Oxfordshire; Text-fig. 3

pacificus, *Shastasaurus*

Paja Formation

Palvennia; Text-fig. 46

Palvennia hoybergeri; Text-fig. 46

panderi, *Dorsoplanites*

panxianensis, *Mixosaurus*

Paraophthalmosaurus

Paraophthalmosaurus kabanovi

[*Paraophthalmosaurus saratoviensis*]

Paraophthalmosaurus saveljeviensis

Paromes Formation

Parvinatator

Parvinatator wapitiensis

Parvipelvia

Pectinatites; Text-fig. 3

Pectinatites elegans; Text-fig. 3

Pectinatites pectinatus; Text-fig. 3

Pectinatites wheatleyensis

pectinatus, *Pectinatites*; Text-fig. 3

periallus, *Mollesaurus*; Text-fig. 46

perrini, *Californosaurus*

Peterborough; Text-fig. 2

Peterborough Member; Text-fig. 3

[*petersonii*, *Microdontosaurus*]

petrinus, *Cymbospondylus*

Petrolacosaurus

Phalarodon

Phalarodon atavus

Phalarodon fraasi

Phantomosaurus

Phantomosaurus neubigi

Pictonia; Text-fig. 3

Pictonia baylei; Text-fig. 3

platydactylus, *Platypterygius*

platyodon, *Temnodontosaurus*

Platypterygiinae

Platypterygius

Platypterygius americanus

Platypterygius australis

'*Platypterygius brunsvicensis*'

Platypterygius hercynicus

Platypterygius platydactylus

Platypterygius sachicarum

[*pleydelli*, *Ophthalmosaurus*]

Pliensbachian

Podmoskaya

popularis, Shonisaurus

Portland Group; Text-fig. 3

Portlandian

Portland Sand Formation; Text-fig. 3

Portland Stone Formation; Text-fig. 3

Posidonia Shale Formation

[*posthumus, Ichthyosaurus*]

[*posthumus, Ichthyosaurus trigonus*]

pseudoscythica, Ilowaiskya

[*pseudoscythica, Otschevia*]

Purbeck Group; Text-fig. 3

Purbeck Limestone Formation; Text-fig. 3

Qianichthyosaurus

Qianichthyosaurus xingyiensis

Qianichthyosaurus zhoui

quadriscissus, Stenopterygius

Queensland

Redwater Shale Member

[*reedi, Baptanodon*]

Ringstead Bay

[*robustus, Baptanodon*]

Rookery Pit

Rope Lake Head

Russia

sachicarum, *Platypterygius*

Saint-Jouin-Bruneval

Salzgitter

Saratov Region

[*saratoviensis*, *Paraophthalmosaurus*]

[*Sauranodon*]

[*Sauranodon discus*]

[*Sauranodon natans*]

[*Sauranodonta*]

saurophagis, *Thalattoarchon*

[*saveljeviensis*, *Ophthalmosaurus*]

saveljeviensis, *Paraophthalmosaurus*; Text-fig. 46

Scalby Formation

Scotland

seeleyi, *Sisteronia*

Seine-Maritime, Département

Shastasaurinae

Shastasaurus

Shastasaurus alexandrae

Shastasaurus pacificus

shawcrossi, *Dearcmhara*

Shonisaurus

Shonisaurus popularis

Shotover

Sierra El Jabalí

Simbirskiasaurus birjukovi

Sisteron

Sisteronia

Sisteronia seeleyi

Sløttsmoya Member

Smallmouth Sands

solei, *Leptonectes*

Solnhofen

Solnhofen Formation

Somerset

Speeton Clay Formation

Spitsbergen

St Clements

St Helens

stellans, *Leninia*

Stenopterygius ; Text-fig. 46

Stenopterygius aaleniensis; Text-fig. 46

‘*Stenopterygius grandis*’

[*Stenopterygius hauffianus*]

[*Stenopterygius longifrons*]

[*Stenopterygius megalorhinus*]

Stenopterygius quadriscissus

Stenopterygius triscissus

Stenopterygius uniter

Stewartby

Stewartby Member; Text-fig. 3

Stonesfield (Slate) Member; Text-fig. 3

Stowbridge

Strawberry Bank

Stretham

Suevoleviathan

Suevoleviathan disinteger

[*sumini*, *Yasykovia*]

Sundance Formation

Sveltonectes

Sveltonectes insolitus

Swanage

Swindon; Text-fig. 2

tangae, *Guizhouichthyosaurus*

Taynton Limestone Formation

Temnodontosaurus

Temnodontosaurus azerguensis

Temnodontosaurus eurycephalus

Temnodontosaurus nuertingensis

Temnodontosaurus platyodon

Temnodontosaurus trigonodon

tenuirostris, *Leptonectes*

Tethys Ocean

Thalattoarchon

saurophagis, *Thalattoarchon*

Thunnosauria

[*thyreospondilus*, *Ophthalmosaurus*]

[*thyreospondybus*, *Ichthyosaurus*]

[*thyreospondylus*, *Ichthyosaurus*]

[*thyreospondylus*, *Macropterygius*]

[*thyreospondylus*, *Ophthalmosaurus*]

tibetensis, *Himalayasaurus*

Tithonian

Toarcian

Toretocnemus

Toretocnemus californicus

Toretocnemus zitteli

Torquirhynchia

Torquirhynchia inconstans

trautscholdi, *Undorosaurus*

Triassic

Triassic, Lower/Early

Triassic, Middle

Triassic, Upper/Late

trigonodon, *Temnodontosaurus*

[*trigonus*, *Ichthyosaurus*]

[*trigonus*, *Macropterygius*]

[*trigonus posthumus*, *Ichthyosaurus*]

triscissus, *Stenopterygius*

typicus, *Hauffiopteryx*

Ulyanovsk Region

'undorensis, *Ophthalmosaurus*'

Undorosaurus; Text-fig. 46

Undorosaurus gorodischensis; Text-fig. 46

Undorosaurus trautscholdi

Undory

United Kingdom

United States

uniter, *Stenopterygius*

Upper Jurassic

Upper Kimmeridge Clay; Text-fig. 3

Upper Oxford Clay (= Weymouth Member); Text-fig. 3

Utatsusaurus

Utatsusaurus hataii

Vaca Muerta Formation

Viking Corridor

Virgatopavlovia; Text-fig. 3

Virgatopavlovia fittoni; Text-fig. 3

Vocontian Basin

volgensis, *Deshayesites*

Volgian

Wabiskaw Member

Wales

wapitiensis, *Parvinatator*

West Melbury Marly Chalk Formation

Weston

West Walton Formation

Westbrooke

Westbury

Weymouth; Text-fig. 2

Weymouth Member; Text-fig. 3

wheatleyensis, *Pectinatites*

Whittlesey

Wiltshire; Text-fig. 3

Wyke Siltstone

Wyoming

xindianensis, *Mixosaurus*

xingyiensis, *Qianichthyosaurus*

Xinminosaurus

Xinminosaurus catactes

yasykovi, *Ophthalmosaurus*; Text-fig. 46

[*yasykovi*, *Yasykovia*]

[*Yasykovia*]

[*Yasykovia kabanovi*]

[*Yasykovia mittai*]

[*Yasykovia sumini*]

[*Yasykovia yasykovi*]

Yetminster

Yorkshire; Text-fig. 3

zhoui, *Qianichthyosaurus*

[*zhuravlevi*, *Brachypterygius*]

[*zhuravlevi*, *Otschevia*]

zitteli, *Toretocnemus*

TEXT-FIGURE CAPTIONS

Text-fig. 37. *Brachypterygius extremus* (Boulenger, 1904): skull (CAMSM J68516) in left lateral view (**a**) and interpretation (**b**). Abbreviations: **an**, angular; **d**, dentary; **en**, external naris; **fr**, frontal; **j**, jugal; **l**, lachrymal; **m**, maxilla; **n**, nasal; **p**, premaxilla; **pf**, postfrontal; **po**, postorbital; **pr**, prefrontal; **qj**, quadratojugal; **sa**, surangular; **sc**, sclerotic plate. Scale bar represents 200 mm. Photograph courtesy Sedgwick Museum, Cambridge, used with permission; illustration by Angela Kirton.

Text-fig. 38. *Brachypterygius extremus* (Boulenger, 1904): complete specimen (BRSMG Ce 16696) in oblique left lateral view. The mounting and display of the specimen preclude taking photographs from a truly orthogonal vantage, so this photo is taken from a viewpoint laterally and slightly ventrally. To show the amount of parallax, two scales are included at the anterior and posterior ends of the specimen. Both of these represent 200 mm. Photograph courtesy Simon Powell/University of Bristol, used with permission.

Text-fig. 39. *Brachypterygius extremus* (Boulenger, 1904): skull (BRSMG Ce 16696) in left lateral view composite photograph (**a**) and interpretation (**b**). The skull is preserved in two portions separated by the line of fracture (**F**): the anterior portion is completely prepared, while the posterior portion has been incompletely prepared, nor does it appear as well preserved. Photographs in a true orthogonal view to the specimen (see also Text-fig. 38) were taken of these two pieces separately and are combined in (**a**). Abbreviations: **F**, fracture line between two blocks of the specimen (thickened line); **an**, angular; **d**, dentary; **en**, external naris; **h?**, possible hyoid bones; **j**, jugal; **l**, lachrymal; **m**, maxilla; **n**, nasal; **p**, premaxilla; **pf**, postfrontal; **po**, postorbital; **pr**, prefrontal; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **sa**,

surangular; **sc**, sclerotic plates; **sp**, splenial; **?**, unidentified element. Scale bar represents 200 mm. Photo courtesy Simon Powell/University of Bristol, used with permission; illustration by Benjamin Moon.

Text-fig. 40. *Brachypterygius extremus* (Boulenger, 1904): posterior skull and anterior trunk (BRSMG Ce 16696) photograph in left lateral view (**a**) and interpretation (**b**), and enlarged interpretation of the right forelimb in ventral view (**c**). Although preserved, the posterior of this portion of the specimen has yet to be fully prepared. Abbreviations: **an**, angular; **c**, coracoid; **d**, dentary; **j**, jugal; **h**, humerus; **hy?**, possible hyoid elements; **i**, intermedium; **ns**, neural spine; **po**, postorbital; **pr**, preaxial accessory element; **pt**, pterygoid; **px**, postaxial accessory element; **q**, quadrate; **qj**, quadratojugal; **r**, radius; **rd**, radiale; **ri**, rib; **s?**, possible scapula; **sa**, surangular; **sc**, sclerotic plate; **sp**, splenial; **u**, ulna; **ul**, ulnare; **vc**, vertebral centrum; **arabic numerals**, distal carpals; **roman numerals**, metacarpals. Scale bars represent 200 mm (**a**, **b**) and 100 mm (**c**). Photograph courtesy Simon Powell/University of Bristol, used with permission; illustration by Benjamin Moon.

Text-fig. 41. *Brachypterygius extremus* (Boulenger, 1904) (CAMSM J68516): basioccipital in posterior (**a**) and left lateral (**b**) views and basisphenoid in ventral view (**c**). Abbreviations: **ac**, articular condyle; **btp**, basiptyergoid process; **icf**, internal carotid foramen; **eca**, extracondylar area; **fex**, exoccipital facet on the basioccipital; **fm**, foramen magnum; **fop**, opisthotic facet on the basioccipital; **fpt**, pterygoid facet on the basisphenoid; **fst**, stapedial facet on the basioccipital; **gr**, groove for transmission of the palatine ramus of the facial (VII) nerve; **no**, notochordal pit; **par**, base of parasphenoid. Scale bar represents 100 mm. Illustrations by Angela Kirton.

Text-fig. 42. *Brachypterygius extremus* (Boulenger, 1904): right forelimbs NHMUK PV R3177 (**a**) and CAMSM J29864 (**b**) in dorsal view; left humerus (WESTM 1978.219) in ventral view (**c**); left humerus (after CAMSM J67556 and WESTM 1978.219) in proximal (**d**) and distal view (**e**). Abbreviations: **dp**, dorsal process; **gr**, marginal groove; **h**, humerus; **i**, intermedium; **if**, intermedial facet on the humerus; **pr**, pre-axial accessory element; **px**, post-axial accessory element; **r**, radius; **rd**, radiale; **rf**, radial facet on the humerus; **u**, ulna; **uf**, ulnar facet on the humerus; **ul**, ulnare; **vp**, ventral (deltopectoral) process of the humerus **arabic numerals**, distal carpals; **roman numerals**, metacarpals; grey area indicates breakage. Scale bars represent 100 mm (**a**, **b**), 50 mm (**c**), and 20 mm (**d**, **e**). Illustrations by Angela Kirton (**a**, **b**) and Benjamin Moon (**c–e**).

Text-fig. 43. *Nannopterygius enthekiodon* (Hulke, 1871): holotype specimen (NHMUK PV 46497) in right lateral view (**a**) and outline interpretation (**b**). Shading marks reconstructed portions. Scale bar represents 500 mm. Photograph courtesy Natural History Museum, London, used with permission; illustration by Benjamin Moon.

Text-fig. 44. *Nannopterygius enthekiodon* (Hulke, 1871): pectoral girdle and fore limb elements (holotype: NHMUK PV 46497) in ventral view (**a**) and interpretation (**b**). Abbreviations: **cl**, clavicle; **lc**, left coracoid; **lh**, left humerus; **ls**, left scapula; **n**, anterior notch of the coracoid; **r**, radius; **rc**, right coracoid; **rh**, right humerus; **rs**, right scapula; **vp?**, probable ventral process (deltopectoral crest) of the humerus; **u**, ulna. Scale bar represents 100 mm. Photograph courtesy Natural History Museum, London, used with permission; illustration by Angela Kirton.

Text-fig. 45. Outline reconstructions of the skull of *Ophthalmosaurus* ‘*Baptanodon*’ *natans* (Marsh, 1879) from the Sundance Formation, Wyoming, USA in right lateral (**a**), dorsal (**b**), ventral (**c**) and posterior (**d**) views. Compare with *Ophthalmosaurus icenicus* (Text-figs 4, 5, 16 in Part 1). Redrawn from Gilmore (1905, 1906). Scale bar represents 250 mm. Illustrations by Benjamin Moon.

Text-fig. 46. Global palaeogeography in the Middle and Late Jurassic (simplified from Blakey 2008, 2014) with ichthyosaur occurrence data from the Paleobiology Database (downloaded 31st January 2014; Alroy 2013a, b) and Bardet *et al.* (2014). Middle Jurassic ichthyosaur occurrences are plotted on a palaeogeographical map of the Bajocian (c. 170 Ma: **a**) and Late Jurassic ichthyosaur occurrences are plotted on a palaeogeographical map of the Tithonian (c. 150 Ma: **b**). Lines of latitude are at 30° intervals. Ichthyosaur remains identified to generic and species level are indicated. Abbreviations: **Ac**, *Arthropterygius chrisorum*; **Ae**, *Aegirosaurus leptospondylus*; **Ar**, *Arthropterygius* sp.; **B**, *Brachypterygius* sp.; **Ba**, *Brachypterygius alekseevi*; **Be**, *Brachypterygius extremus*; **Ca**, *Caypullisaurus bonapartei*; **Cc**, *Chacaicosaurus cayi*; **Cr**, *Cryptopterygius kristiansenae*; **Mp**, *Mollesaurus periallus*; **N**, *Nannopterygius enthekiodon*; **O**, *Ophthalmosaurus* sp.; **Oi**, *Ophthalmosaurus icenicus*; **On**, *Ophthalmosaurus natans*; **Oy**, *Ophthalmosaurus yasykovi*; **P**, *Palvennia hoybergeti*; **Ps**, *Paraophthalmosaurus saveljeviensis*; **Sa**, *Stenopterygius aaleniensis*; **Ug**, *Undorosaurus gorodischensis*; **Ut**, *Undorosaurus trautscholdi*; question marks indicate uncertainty; unlabelled occurrences are not identifiable to genus level or lower.

TABLE CAPTIONS

Table 5. Specimens referable to *Brachypterygius extremus* (Boulenger, 1904).

Abbreviations: **Cambs**, Cambridgeshire; **KCF**, Kimmeridge Clay Formation; **Oxon**, Oxfordshire; **PSF**, Portland Stone Formation; **Wilts**, Wiltshire.

Table 6. Selected measurements (in mm) of material referred to *Brachypterygius extremus* (Boulenger, 1904).

Table 7. Measurements (in mm) of the width of the extracondylar area of basioccipitals referred to *Brachypterygius extremus* (Boulenger, 1904). Compare with *Ophthalmosaurus icenicus* Seeley, 1874b in Table 4 in Part 1.

Table 8. Dimensions (in mm) of humeri referred to *Brachypterygius extremus* (Boulenger, 1904). WESTM 1978.219 may be the contralateral forelimb of the holotype (NHMUK PV R3177). Abbreviations: **L**, left; **R**, right.

Table 9. Measurements (in mm) of distal facets of humeri referred to *Brachypterygius extremus* (Boulenger, 1904). WESTM 1978.219 may be the contralateral forelimb of the holotype (NHMUK PV R3177). Abbreviations: **L**, left; **R**, right.

Table 10. Specimens historically referred to *Nannopterygius enthekiodon* (Hulke, 1871). Specimens for which the referral is uncertain or doubtful are indicated with a question mark. Abbreviations: **Cambs**, Cambridgeshire; **KCF**, Kimmeridge Clay Formation; **OCF**, Oxford Clay Formation; **Wilts**, Wiltshire.

Table 11. Comparison of skull features defined by Appleby (1956, p. 442) to distinguish *Baptanodon* (= *Ophthalmosaurus natans*) from *Ophthalmosaurus icenicus*.

Table 12. Character differences between *Ophthalmosaurus icenicus* and *Ophthalmosaurus natans* from the studies of Druckenmiller & Maxwell (2010) and Fischer *et al.* (2013). Character numbers are those referred to in the text. The reference column refers to the original paper (DM, Druckenmiller & Maxwell 2010; F, Fischer *et al.* 2013) followed by the character in that matrix.

PLATE 31

Fig.

Page

Brachypterygius extremus (Boulenger, 1904)

Kimmeridge Clay Formation of Mepal, Cambridgeshire.

- 1, 2 Left parietal (CAMSM X39251bj) in dorsal and ventral views.
- 3, 4 Left postfrontal (CAMSM X39251ai) in dorsal and ventral views.
- 5, 6 Left supratemporal (CAMSM X39251bt) in dorsal and ventral views.
- 7, 8 Left quadratojugal (CAMSM X39251) in lateral and medial views.

Scale bars represent 50 mm.

PLATE 32

Fig.

Page

Brachypterygius extremus (Boulenger, 1904)

Kimmeridge Clay Formation of Mepal, Cambridgeshire.

- 1, 2 Right vomer (CAMSM X39251) in lateral and medial views (anterior is to the left).
- 3, 4 Right pterygoid and stapes (CAMSM X39251bh) in dorsal and ventral views (anterior is to the top).
- 5–7 Right quadrate (CAMSM X39251) in posterior, lateral, and medial views.
- 8, 9 Sclerotic plate (CAMSM X39251bn) in external and internal views.
- 10, 11 Two articulated sclerotic plates (CAMSM X39251bo) in external(?) and internal (?) views.

Scale bars represent 50 mm (figs 1–7, 10, 11) and 20 mm (figs 8, 9).

PLATE 33

Fig.

Page

Brachypterygius extremus (Boulenger, 1904)

Kimmeridge Clay Formation (*wheatleyensis* zone) of Stowbridge, Norfolk.

- 1–4 Basisphenoid (CAMSM TN571.11 = J68516) in anterior, posterior, dorsal, and ventral views.
- 5–8 Basioccipital (CAMSM TN571.11 = J68516) in anterior, posterior, ventral, and dorsal views.

Scale bars represent 50 mm.

PLATE 34

Fig.

Page

Brachypterygius extremus (Boulenger, 1904)

Kimmeridge Clay Formation of Mepal, Cambridgeshire.

- 1–4 Basisphenoid (CAMSM X39251ae) in anterior, posterior, dorsal, and ventral views.
- 5, 6 Right(?) prootic (CAMSM X39251ce) in external (anterior) and internal (posterior) views.
- 7–12 Right opisthotic (CAMSM X39251as) in anterior, posterior, dorsal, ventral, lateral, and medial views.

Scale bars represent 50 mm (figs 1–4, 7–12) and 20 mm (figs 5, 6).

PLATE 35

Fig.

Page

Brachypterygius extremus (Boulenger, 1904)

Kimmeridge Clay Formation of Mepal, Cambridgeshire.

- 1–4 Supraoccipital (CAMSM X39251bt) in anterior, posterior, dorsal, and ventral views.
- 5, 6 Left angular (CAMSM X39251) in lateral and medial views (anterior is to the top).
- 7, 8 Right articular (CAMSM X39251ar) in medial and lateral views.

Scale bars represent 50 mm.

PLATE 36

Fig.

Page

Brachypterygius extremus (Boulenger, 1904)

Kimmeridge Clay Formation of Mepal, Cambridgeshire.

- 1, 2 Left surangular (CAMSM X39251aa, anterior portion) in lateral and medial views.
3, 4 Left surangular (CAMSM X39251y, posterior portion) in lateral and medial views.
5, 6 Right surangular (CAMSM X39251ak, anterior portion) in lateral and medial views.
7, 8 Right surangular (CAMSM X39251cf, posterior portion) in lateral and medial views.
9, 10 Left prearticular (CAMSM X39251cb, portion) in lateral and medial views.

Scale bars represent 50 mm. Figures 1 and 2, 3 and 4, 5 and 6, and 7 and 8 are oriented approximately correctly, but are not in their true relative positions. Anterior is to the top.

PLATE 37

Fig.

Page

Brachypterygius extremus (Boulenger, 1904)

Kimmeridge Clay Formation of Mepal, Cambridgeshire.

1–3 Tooth (CAMSM X39251c) in labial, lingual, and mesial or distal views.

4–6 Tooth (CAMSM X39251h) in labial, lingual, and medial or distal views.

7–9 Tooth (CAMSM X39251p) in labial, lingual, and mesial or distal views.

10, 11 Right clavicle (CAMSM X39251ag) in anterior and posterior views.

12, 13 Left clavicle (CAMSM X39251aj) in anterior and posterior views.

14, 15 Left scapula (CAMSM X39251an) in lateral and medial views.

Scale bars represent 20 mm (figs 1–9) and 50 mm (figs 10–15).

PLATE 38

Fig.

Page

Brachypterygius extremus (Boulenger, 1904)

Kimmeridge Clay Formation of Ely, Cambridgeshire (figs 1–3) and Smallmouth Sands,
Dorset (fig. 4).

1–3 Left humerus (CAMSM J67556) in dorsal, ventral, and distal views.

4 Left forelimb (WESTM 1978.219) in dorsal view (anterior is to the bottom).

Scale bars represent 50 mm (figs 1–3) and 100 mm (fig. 4).

PLATE 39

Fig.

Page

Nannopterygius enthekiodon? (Hulke, 1871)

Kimmeridge Clay Formation of Kimmeridge Bay, Dorset.

- 1–5 Hindlimb (NHMUK PV 46497a) in dorsal, ventral, proximal, anterior, and posterior views.

Ichthyosauria indet.

Oxford Clay Formation of Fletton, Cambridgeshire.

- 6–8 Three cervical vertebral centra (NHMUK PV R5832) in anterior, dorsal, and left lateral views.

Scale bars represent 50 mm.

PLATE 40

Fig.

Page

Macropterygius sp. indet.

Kimmeridge Clay Formation of the Isle of Portland, Dorset (figs 1–3) and St Helens,
Oxfordshire (figs 4–6).

- 1–3 Left humerus (NHMUK PV 42286) in dorsal, ventral, and distal views.
4–6 Right humerus (OUMNH J68534) in dorsal, ventral, and distal views.

Scale bars represent 50 mm.